UNIVERSIDADE VILA VELHA - ES

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DE ECOSSISTEMAS

Trichodactylus fluviatilis (DECAPODA, TRICHODACTYLIDAE) E O PROCESSAMENTO DE MATÉRIA ORGÂNICA EM ECOSSISTEMAS LÓTICOS

LARISSA CORTELETTI DA COSTA FERREGUETTI

VILA VELHA

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Orientador

Grandes descobertas científicas são realizadas a partir de um olhar profundo sobre aquilo que se parece óbvio à primeira vista.

Autor desconhecido

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SUMÁRIO

RESUMO

FERREGUETTI, Larissa Corteletti da Costa, Dr., Universidade Vila Velha – ES, Março de 2018. ***Trichodactylus fluviatilis* (Decapoda, Trichodactylidae) e o processamento de matéria orgânica em ecossistemas lóticos.** Orientador: Prof. Dr. Marcelo da Silva Moretti.

Esta tese teve como objetivo avaliar a influência do caranguejo dulcícola, *Trichodactylus fluviatilis*, no processamento de matéria orgânica em ecossistemas lóticos. Partindo do pressuposto que estes crustáceos são onívoros, i.e., se alimentam tanto de detritos orgânicos quanto de presas vivas, foi hipotetizado que a qualidade e a disponibilidade de recursos alimentares influenciam a preferência alimentar destes organismos e, consequentemente, as taxas de processamento de detritos foliares. Esta tese é composta por três capítulos e apresenta resultados obtidos em campo e em experimentos de laboratório realizados com a espécie de caranguejo estudada e insetos fragmentadores encontrados associados a detritos foliares em decomposição em riachos de Mata Atlântica. No Capítulo 1 as relações comprimento-biomassa de duas populações de *T. fluviatilis* foram descritas utilizando diferentes modelos matemáticos (linear, exponencial e *power*) e variáveis corporais (comprimento e largura da carapaça). Os resultados obtidos corroboraram o uso das duas variáveis da carapaça como preditores da biomassa de *T. fluviatilis* e a necessidade de se determinar uma relação para cada população estudada. Além disso, a mesma relação pode ser utilizada para indivíduos de ambos os sexos. No Capítulo 2 foram determinados o conteúdo estomacal de *T. fluviatilis* e as taxas de processamento de detritos foliares em ensaios de laboratório contendo caranguejos e larvas dos insetos fragmentadores *Triplectides* sp., juntos e separados. Os resultados obtidos suportam a potencial participação de *T. fluviatilis* na decomposição de detritos foliares e demonstraram que, apesar da elevada abundância de algas e matéria orgânica particulada fina no conteúdo estomacal, os adultos desta espécie podem se alimentar tanto de detritos foliares quanto das larvas de *Triplectides* sp. No entanto, as taxas de processamento não diferiram entre os tratamentos. No Capítulo 3 foi avaliado a capacidade de fragmentação e o comportamento alimentar de *T. fluviatilis* na presença de diferentes detritos foliares e insetos fragmentadores. Foram oferecidos aos caranguejos detritos foliares que apresentam diferenças em suas características físicas e químicas (*Hoffmannia dusenii*, *Miconia chartacea*, *Myrcia lineata* e *Eucalyptus globulus*) e larvas de dois invertebrados fragmentadores que constroem abrigos com diferentes materiais (*Phylloicus major* e *Triplectides gracilis*). Apesar dos indivíduos de *T. fluviatilis* terem escolhido os itens alimentares de forma aleatória, a predação das larvas de *P. major* por *T. fluviatilis* foi maior que a das larvas de *T. gracilis*. Os resultados obtidos indicaram que os caranguejos fragmentam detritos com qualidades físico-químicas inferiores, recursos esses muitas vezes rejeitados pelos fragmentadores típicos de ambientes lóticos. Os resultados desta tese reforçam a importância dos caranguejos dulcícolas no processamento de detritos foliares e contribuem para o maior entendimento do papel desta espécie nas relações tróficas em riachos de Mata Atlântica.

PALAVRAS-CHAVE: Macroconsumidores, detritos foliares, invertebrados fragmentadores, comportamento alimentar, riachos de Mata Atlântica.

ABSTRACT

FERREGUETTI, Larissa Corteletti da Costa, Dr., University of Vila Velha – ES, March 2018. ***Trichodactylus fluviatilis*** **(Decapoda, Trichodactylidae) on the processing of organic matter in lotic ecossystems** Supervisor: Dr. Marcelo da Silva Moretti.

This thesis aimed to evaluate the influence of the freshwater crab, *Trichodactylus fluviatilis*, on the processing of organic matter in lotic ecosystems. Based on the assumption that these crustaceans are omnivorous, i.e., they feed on both organic detritus and live prey, we hypothesized that the quality and availability of food resources influence the food preference of these organisms and, consequently, the decay rates of leaf litter. The thesis is composed of three chapters and presents the results obtained in the field and in laboratory experiments carried out with the crab species studied and shredder insects found associated to decomposing leaf litter in Atlantic Forest streams. In Chapter 1 the size-mass relationships of two populations of *T. fluviatilis* were described using different mathematical models (linear, exponential and power) and body variables (carapace length and width). The obtained results corroborated the use of the two carapace variables as predictors of the biomass of *T. fluviatilis* and the need to determine a relationship for each studied population. In addition, the same relationship can be used for individuals of both sexes. In Chapter 2, the gut contents of *T. fluviatilis* and the decay rates of leaf litter were determined in laboratory trials containing crabs and larvae of the insect shredder *Triplectides* sp., alone and together. The results support the potential participation of *T. fluviatilis* on the decomposition of leaf litter and demonstrated that, in spite of the high abundance of algae and fine particulate organic matter in the gut contents, the adults of this species can feed on both leaf litter and larvae of *Triplectides* sp. However, decay rates did not differ between treatments. In Chapter 3 the shred capacity and feeding behavior of *T. fluviatilis*, when exposed to different leaves and insect shredders, were evaluated. Leaf species with different physical and chemical characteristics (*Hoffmannia dusenii*, *Miconia chartacea*, *Myrcia lineata* and *Eucalyptus globulus*) and larvae of two shredders that build their shelters with different materials (*Phylloicus major* and *Triplectides gracilis*) were offered to crabs. Although the individuals of *T. fluviatilis* chose food items randomly, the predation of larvae of *P. major* by *T. fluviatilis* was higher than that of larvae of *T. gracilis*. The results indicated that the crabs could shred low quality leaves, resources that are often rejected by typical insect shredders. The results of this thesis reinforce the importance of freshwater crabs on the processing of leaf litter and contribute to a better understanding of the role of this species in the trophic relationships in Atlantic Forest streams.

KEY WORDS: Macroconsumers, leaf litter, invertebrate shredders, feeding behavior, Atlantic Forest streams.

INTRODUÇÃO GERAL

Em riachos sombreados, a matéria orgânica produzida pela vegetação ripária representa uma importante fonte de energia e carbono para as comunidades aquáticas (Vannote *et al.*, 1980; Wallace *et al*., 1997). A matéria orgânica é constituída principalmente por detritos foliares, os quais podem ser utilizados como recurso direto ou indireto por organismos detritívoros (Cheshire *et al.,* 2005; Gonçalves *et al.,* 2006). Desta forma, o detrito é incorporado no ecossistema aquático promove o fornecimento de recursos alimentares, abrigo e habitat para os organismos heterotróficos (Cummins *et al*., 1973; Kobayashi & Kagaya 2005; Tiegs *et al*., 2008).

Os organismos detritívoros, principalmente os invertebrados fragmentadores, são responsáveis por grande parte do processamento de matéria orgânica em riachos (Suberkropp, 1992; Graça, 2001). Esses organismos reduzem este material em pequenas partículas e a disponibilizam para outros grupos tróficos localizados à jusante (Cummins *et al*., 1989). Desta forma, os fragmentadores constituem um importante *link* nas teias alimentares de riachos, sendo considerados organismos facilitadores (Graça, 2001).

Determinados grupos pertencentes às ordens Trichoptera, Plecoptera e Diptera têm sido considerados como os principais organismos fragmentadores de matéria orgânica em riachos temperados (Cheshire *et al*., 2005; Ferreira *et al*., 2012; Tonin *et al*., 2014). Entretanto, a importância de invertebrados fragmentadores nas regiões tropicais vem sendo amplamente discutida, uma vez que alguns estudos têm encontrado uma baixa abundância e/ou participação de insetos fragmentadores nos processos ecológicos (Mathuriau & Chauvet, 2002; Cheshire *et al*., 2005; Gonçalves *et al*., 2006; Boyero *et al*., 2012). Boyero *et al*. (2009) ressaltaram que a menor abundância destes organismos em alguns riachos tropicais não necessariamente resulta em menores taxas de decomposição, uma vez que a influência de alguns grupos de macroconsumidores, como crustáceos e peixes, têm sido negligenciada devido a equívocos em sua classificação trófica.

Mais recentemente, alguns estudos sugeriram que a presença de grandes consumidores onívoros compensaria a menor abundância de insetos especializados na fragmentação de detritos foliares em ecossistemas aquáticos tropicais (Li & Dudgeon, 2008). Além disso, a maior biomassa desses macroconsumidores resultaria em uma maior eficiência no processamento de detritos foliares quando comparados aos insetos fragmentadores (Moss, 2004). Por exemplo, Usio (2000) observou que um lagostim do gênero *Paranephrops* (Decapoda, Parastacidae) aumentou significativamente as taxas de decomposição de detritos foliares em um riacho na Nova Zelândia, sobrepondo o efeito dos demais fragmentadores. No Brasil, alguns estudos sugeriram que os crustáceos dulcícolas contribuem para o processamento da matéria orgânica, sendo que taxas de decomposição mais elevadas foram observadas na presença desses organismos (Landeiro *et al.*, 2008; Moulton *et al.,* 2010).

A presença de macroconsumidores também pode influenciar as taxas de processamento dos detritos orgânicos através da sua interação com os demais invertebrados fragmentadores. Por serem onívoros, estes organismos podem exercer uma pressão de predação sobre os fragmentadores de menor tamanho (Oberndorfer *et al.*, 1984). Cogo *et al.* (2014) demonstraram que a predação exercida por *Aegla longirostri* (Decapoda, Aeglidae) reduziu a abundância de organismos das ordens Trichoptera, Ephemeroptera, Diptera (Chironomidae) nas assembleias associadas a detritos foliares. Além disso, a presença de macroconsumidores pode influenciar o comportamento e os padrões de colonização dos detritos pelas assembleias de invertebrados aquáticos (Usio, 2000).

Os invertebrados aquáticos, como as larvas das espécies *Triplectides gracilis*, 1839 (Trichoptera, Leptoceridae) e *Phylloicus major*, 1880 (Trichoptera, Calamoceratidae)*,* e os caranguejos da espécie *Trichodactylus fluviatilis* Latreille, 1828 (Decapoda, Trichodactylidae) são abundantes em determinados riachos tropicais, e estão presentes em corpos hídricos com drenagem Atlântica. As larvas de Trichoptera são fragmentadoras de detritos orgânicos, utilizando estes recursos para construção de abrigos e alimentação. Desta forma, estes organismos constituem um importante componente do processamento de detritos foliares nestes ambientes (Becker *et al.*, 2009; Boyero *et al.*, 2011). Ferro & Sites (2007) observaram que estes organismos são também utilizados como recurso alimentar por macroconsumidores, como os indivíduos de *T. fluviatilis*. De acordo com Collins *et al.* (2006), estes caranguejos são onívoros com um amplo espectro trófico que varia desde algas e detritos foliares até larvas de insetos e vertebrados. Desta forma, podem atuar como fragmentadores (Williner *et al.*, 2014) e predadores (Lima *et al.*, 2013). Devido a baixa abundância de insetos fragmentadores em alguns riachos neotropicais e a capacidade dos caranguejos dulcícolas em consumir detritos foliares, a presença destes macroconsumidores pode influenciar de maneira significativa a decomposição foliar nestas regiões.

Os experimentos apresentados nesta tese avaliaram as relações comprimento-biomassa, a capacidade de fragmentação e o comportamento alimentar do crustáceo dulcícola *Trichodactylus fluviatilis* no sudeste do Brasil, e estão divididos em 3 capítulos. No Capítulo 1 foram descritas as equações comprimento-biomassa para três medidas corporais de duas populações pertencentes à diferentes bacias hidrográficas, utilizando-se três modelos matemáticos. No Capítulo 2 foram analisados o conteúdo estomacal de *T. fluviatilis* e a influência que esse macroconsumidor exerce sobre o processo de decomposição de matéria orgânica. Foram avaliados a capacidade de fragmentação, taxas de consumo e produção de MOPF de *T. fluviatilis* e estas foram comparadas a outro invertebrado fragmentador típico (*Triplectides gracilis*), quando expostas a detritos foliares com diferentes componentes estruturais e químicos. O Capítulo 3 foi dividido em dois experimentos laboratoriais. O primeiro avaliou-se a capacidade de fragmentação de *T. fluviatilis* através da exposição destes organismos a detritos foliares de diferentes qualidades. E o segundo, o comportamento alimentar de *T. fluviatilis*, na presença de detritos foliares que apresentam diferentes qualidades e dois invertebrados fragmentadores que constroem abrigos com materiais diferentes (*Phylloicus major* e *T. gracilis*).

HIPÓTESE E OBJETIVOS

Hipótese

Partindo do pressuposto que os indivíduos de *T. fluviatilis* são onívoros, i.e., se alimentam tanto de detritos orgânicos quanto de presas vivas, foi hipotetizado que a qualidade e a disponibilidade de recursos alimentares influenciam a preferência alimentar destes organismos e, consequentemente, as taxas de processamento de detritos foliares.

Objetivo geral

Avaliar a influência do caranguejo dulcícola *Trichodactylus fluviatilis* no processamento de matéria orgânica em ecossistemas lóticos em riachos de Mata Atlântica.

Objetivos específicos

- Determinar as relações comprimento-biomassa dos indivíduos de *T. fluviatilis* utilizando diferentes modelos matemáticos (linear, exponencial e *power*) e variáveis corporais (comprimento e largura da carapaça).
- Analisar o conteúdo estomacal de *T. fluviatilis* e a verificar a influência que esse macroconsumidor exerce sobre o processo de decomposição de matéria orgânica.
- Avaliar a capacidade de fragmentação e o comportamento alimentar de *T. fluviatilis* na presença a diferentes detritos foliares e insetos fragmentadores.

CAPÍTULO 1

Size-mass relationships of *Trichodactylus fluviatilis* (Decapoda, Trichodactylidae): An important macroconsumer in coastal streams of the Atlantic Forest

Larissa Corteletti da Costai, Walace Pandolpho Kiffer Junior, Cinthia Gabriela Medeiros & Marcelo S. Moretti

Size-mass relationships of *Trichodactylus fluviatilis* (Decapoda, Trichodactylidae): An important macroconsumer in coastal streams of the Atlantic Forest

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ABSTRACT

Size-mass relationships are widely used to estimate the biomass of organisms preserved for taxonomic purposes or kept alive in laboratory experiments. The objective of this study was to determine the size-mass relationships for two populations of *Trichodactylus fluviatilis* found in the Atlantic Forest (Southeast Brazil). Different mathematical models (linear, exponential, and power) and body variables (carapace length [CL] and width [CW]) were used to determine the equations with the best predictive powers. Totals of 45 and 50 specimens were collected from the Macuco and Mestre Álvaro streams, respectively. The values of the body variables and biomasses did not differ between the sexes or the populations studied. The best relationships to estimate the biomass of *T. fluviatilis* were determined with the power model, both in the Macuco ($r^2 = 0.89$ [CL] and 0.90 [CW]) and Mestre Álvaro streams ($r^2 = 0.94$ for both body variables). The exponential and linear models determined equations with good ($r^2 > 0.80$) and moderate ($0.80 \geq r^2 \geq 0.60$) predictive powers, respectively. Considering only the power model, the size-mass relationships determined separately for males and for the population sampled in Mestre Álvaro had the best predictive powers. The slopes of the equations determined by both body variables did not differ between the sexes in either stream, but differences were observed between the populations studied. The obtained results corroborated the use of carapace length and width as predictors of the biomass of *T. fluviatilis* and the need to determine one relationship for each population studied. Additionally, one single equation can be used for individuals of both sexes. The estimation of the biomass of *T. fluviatilis* through size-mass relationships constitutes an important contribution to the evaluation of the functional role of these macroconsumers in the detritus-based food webs of Atlantic Forest streams.

KEY WORDS: Atlantic Forest streams, biomass estimation, body dimensions, freshwater crabs, mathematical models.

INTRODUCTION

Values of biomass constitute an important variable in the evaluation of the participation of biota in different phases of aquatic metabolism, such as production, consumption and decomposition of organic matter (Benke, 1996; Cressa, 1999; Méthod *et al*., 2012). Traditionally, values of abundance and density have been used to determine the ecological importance of populations (Downing & Rigler, 1984; Cyr *et al*., 1997; Stoffles *et al*., 2003). However, due to differences in size often observed among individuals of different species, values of biomass are more appropriate for assessing the role of a population in an ecosystem (Burgherr & Meyer, 1997; Cyr *et al*., 1997), especially in relation to trophic structure and energy flow (Woodward & Hildrew, 2002; Tonin *et al*., 2014). The biomass of a population is related to the physiological and ecological aspects of its organisms. Therefore, biomass can be influenced by life history (Brand & Miserendino, 2012), seasonal distribution patterns (Schmid *et al*., 2000), trophic interactions (Cohen *et al*., 2005) and morphological changes related to sexual maturity (Woodward *et al*., 2005).

The determination of the biomass of aquatic invertebrates can be performed by a direct measurement of the dry mass of the organisms (Méthot *et al*., 2012; Morante *et al*., 2012) or by indirect methods such as estimates via biovolume (Morin & Nadon, 1991) and size-mass relationships (Burgherr & Meyer, 1997; Benke *et al*., 1999; Cressa, 1999). The broad use of size-mass relationship has some advantages, such as the reduction in possible errors caused by the variation in biomass of preserved organisms (Cressa, 1999; Johnston & Cunjak, 1999; Edwards *et al*., 2009) and not having to not destroy the organisms analyzed (Towers *et al*., 1994; Von Schiller & Solimini, 2005; Méthot *et al*., 2012). In addition to body length (Burgherr & Meyer, 1997; Benke *et al*., 1999; Cressa, 1999) or carapace size in the case of decapods (Pinheiro & Fransozo, 1993), different body dimensions can also be used as predictors of the biomass of aquatic invertebrates, such as distance between eyes (Becker *et al*., 2009), tibia length (Kiffer *et al*., 2016) and cheliped length (Blackstone, 1986), which facilitates the measurement process. Therefore, size-mass relationships allow the determination of biomass for organisms preserved for taxonomic purposes (Genkai-Kato & Miyasaka, 2007) or kept alive in laboratory experiments (Kiffer *et al*., 2016). According to Stoffels *et al*. (2003), the estimation of biomass via body dimensions is generally simple, fast and accurate when compared to other methods. However, since size-mass relationships have high specificity, it is recommended that one equation be determined for each population studied (Johnston & Cunjak, 1999; Kimmerer *et al*., 2005; Martins *et al*., 2014). Furthermore, in species with different growth patterns for males and females, size-mass relationships should be determined separately for both sexes (Silva *et al*., 2014).

Size-mass relationships have been used to estimate the biomass of aquatic invertebrates found worldwide, and most of these relationships were determined for the immature stages of insects (see Smock, 1980; Meyer, 1989; Burgherr & Meyer, 1997; Benke *et al*., 1999; Johnston & Cunjak, 1999; Giustini *et al*., 2008; De Figueroa *et al*., 2009). In tropical streams, taxa belonging to the orders Ephemeroptera, Plecoptera and Trichoptera have the highest number of relationships described (Towers *et al*., 1994; Cressa, 1999; Becker *et al*., 2009; Martins *et al*., 2014; Kiffer *et al*., 2016). Despite the importance of freshwater decapods to the energetic metabolism of some lotic ecosystems (Moulton *et al*., 2010; Williner & Collins, 2013; Williner *et al*., 2014), few studies have determined size-mass relationships for freshwater crabs and shrimp (but see Mansur *et al*., 2005; Lima *et al*., 2013).

Recently, the role of macroconsumers in the decomposition of organic matter in streams has received more attention (Williner & Collins, 2013; Williner *et al*., 2014; Costa *et al*., 2016). Moulton *et al*. (2010) demonstrated that crabs and shrimp can significantly influence leaf mass loss because the largest body size of these organisms in relation to other detritivores may result in high rates of consumption *per capita* (Moss, 2004). In addition, these organisms may also feed on insects that shred organic matter, decreasing the decomposition rates (Cogo & Santos, 2013; Cogo *et al*., 2014). In this context, the estimation of the biomass of macroconsumers is important for the development of experiments aiming to evaluate the actual participation of these organisms in the decomposition of leaf litter (Thongtham *et al*., 2008) and, consequently, nutrient cycling and energy flow in lotic ecosystems (Yeo *et al*., 2008).

Crabs in the family Trichodactylidae are omnivorous and can feed on algae, organic matter, invertebrates and small vertebrates (Cumberlidge *et al*., 2009; Burress *et al*., 2013; Costa *et al*., 2016). In the coastal streams of the Atlantic Forest, the species *Trichodactylus fluviatilis* Latreille, 1828 is commonly found in leaf patches formed on the streambed, where insect shredders of the genera *Triplectides* Kolenati, 1859 (Leptoceridae) and *Phylloicus* Müller, 1880 (Calamoceratidae) also occur in abundance (Baptista *et al*., 2001; Costa *et al*., 2016; Mendes *et al*., 2017). In these ecosystems, this species represents an important component of detritus-based food webs and can influence both the taxonomic structure of aquatic communities and the decomposition of organic matter (Collins *et al*., 2006; Teodósio & Masunari, 2009;

Williner *et al*., 2009; Costa *et al*., 2016).

The objective of this study was to determine the size-mass relationships for adult crabs of the species *T. fluviatilis*. To make this determination, different mathematical models (linear, exponential and power) and body variables (carapace length and width) were used to determine the equations that have the best predictive powers for males, females, and both sexes together. The relationships were determined for two populations that have been studied to better understand the feeding behavior and life history of this species in Atlantic Forest streams.

MATERIALS AND METHODS

Study area

Specimens of *T. fluviatilis* were collected from the Macuco (20º01’23.1” S, 40º32’58.6” W; 593 m a.s.l.) and Mestre Álvaro streams (20º09’00.2” S, 40º18’49.1” W; 251 m a.s.l.), which are located in the central region of the state of Espírito Santo (Southeast Brazil), approximately 50 km from the coast. These streams were chosen because they are inside fragments of the Atlantic Forest and present large leaf patches colonized by different taxa of aquatic invertebrates (Mendes *et al*., 2017). In the two reaches studied, the streambed was formed by slightly inclined rapids interspersed by large pools. The riparian vegetation was well developed, with shade covering approximately 80% of the streambed, and the substrate was heterogeneous, composed of pebbles, gravel, sand and leaf patches. More information about the study area and the abiotic parameters of the Macuco and Mestre Álvaro streams can be found in the study by Mendes *et al*. (2017).

Size-mass relationships

To determine the size-mass relationships, 45 (31 males and 14 females) and 50 (36 males and 14 females) adult individuals of *T. fluviatilis* were collected manually in the Macuco and Mestre Álvaro streams, respectively. The organisms of each stream were placed separately in coolers containing stream water and were transported on the same day to the laboratory, where they were sexed and measured. The carapace length (CL) was determined by the distance between the rostral sinus and the central portion of the posterior margin, while the carapace width (CW) was determined by the largest distance between the lateral edges of the carapace (Lima *et al*., 2013). Body variables were measured with a digital caliper (0.1 mm). After the measurements, the organisms were individually placed in preweighed aluminum pans and dried at 60° C for 72 h. The samples were then cooled in a desiccator for 1 h and weighed on an analytical balance (0.01 mg).

Data analysis

To determine the best relationships between the body variables and the biomass of *T. fluviatilis*, linear (1), exponential (2) and power (3) models or their equivalent logarithms were used:

$$DM = a + b \, . \, L \tag{1}$$

$$DM = a \, . \, e^{bL} \text{ (in linear form: } \ln DM = \ln a + b \, . \, L) \tag{2}$$

$$DM = a \, . \, L^{b} \text{ (in linear form: } \ln DM = \ln a + b \, . \ln L) \tag{3}$$

where a/b are constants of the regression, DM is the dry mass, L is the body variable (CL, CW) and e is a mathematical constant (Euler's number: 2.718).

The fit of the regression equations was analyzed by the coefficient of determination (r^2), significance level (p, obtained by regression ANOVA) and analysis of residuals. According to Kiffer *et al*. (2016), the equations whose values of $r^2 > 0.80$ were considered those with a good predictive power, and $0.60 \leq r^2 \leq 0.80$ indicated moderate predictive power. None of the equations determined in this study had a low predictive power ($r^2 < 0.60$).

Data on carapace length, carapace width and biomass were compared across sexes in each stream and across the populations studied by the Kruskal–Wallis test, a non-parametric analysis of variance, because of the differences in the number of males and females sampled (Zar, 2010). The slopes of the regression equations determined for each body variable with the model that presented the best fit (power) were compared across sexes in each stream and across the populations studied by analysis of covariance (ANCOVA). All the data had their normality and homogeneity of variances tested. Statistical analyses were performed with R software (R Core Development Team, 2013) and based on Zar (2010).

RESULTS

In Macuco, the biomass of the individuals ranged from 1.25 to 6.07 g in males and from 1.88 to 3.41 g in females; in Mestre Álvaro, these values ranged from 1.30 to 8.42 g in males and 1.34 to 6.07 g in females (Table 1). The coefficients of variation of the values of biomass were higher in males (59.7 and 70.5%) and in the population sampled in Mestre Álvaro (64.1%). In terms of body variables, the values of carapace length and width had smaller variations than biomass (Macuco: 1.86 - 2.75 and 0.98 - 3.01 cm, respectively; Mestre Álvaro: 1.30 - 3.00 and 0.40 - 3.30 cm, respectively), and the coefficients of variation of the two variables were similar within males, females, and both sexes together (Table 1). The coefficients of variation of the body variables CL and CW were also higher in males (Macuco: 24.2 and 23.8%, respectively, and Mestre Álvaro: 31.7 and 32.5%, respectively) and in the population sampled in Mestre Álvaro (29.0 and 29.1%, respectively). However, the values of carapace length, carapace width and biomass did not differ between sexes in the two studied streams nor in the populations studied (Table 2).

The body variables determined the size-mass relationships with a high significance level in the three mathematical models ($p < 0.001$; Table 3). Using data for both sexes together, the best relationships to estimate the biomass of *T. fluviatilis* were determined using the power model in Macuco ($r^2 = 0.89$ and 0.90 for CL and CW, respectively) and in Mestre Álvaro ($r^2 = 0.94$ for both body variables). The exponential model also determined equations with a good predictive power in the two streams (Macuco: $r^2 = 0.87$ for both body variables; Mestre Álvaro: $r^2 = 0.86$ and 0.85 for CL and CW, respectively), while the linear model determined equations with a moderate predictive power ($0.76 \leq r^2 \leq 0.80$).

The comparisons across the equations determined for males and females separately were conducted using only the power model. The size-mass relationships determined for males had the best predictive powers (Table 3). In addition, the highest coefficients of determination were obtained for the male individuals sampled in Mestre Álvaro ($r^2 = 0.95$ and 0.94 for CL and CW, respectively). The slopes of the equations determined by carapace length and width did not differ between the sexes in the two streams, but differences were observed between the populations studied (Table 4). Figure 1 shows the relationships of the biomass of *T. fluviatilis* as a function of carapace length and width in the Macuco and Mestre Álvaro streams.

DISCUSSION

The body variables used in the present study determined equations with good and moderate predictive powers for both sexes and populations of *T. fluviatilis*. Wenzel *et al*. (1990) suggested that only the body variables that determine equations with a predictive power higher than to 80% should be used to estimate biomass. Carapace length and width are variables frequently used in studies with crustaceans because they are considered good predictors of the biomass of these organisms (Sukumaran & Neelakantan, 1997; Pinheiro & Taddei, 2005; Lima *et al*., 2013). Moreover, these variables are easily measured *in situ* (Diawol *et al*., 2016) and do not require transport of the individuals to the laboratory (Dobson *et al*., 2007). The dimensions of the carapace have been used to evaluate species biological and ecological functions, such as relative growth, sexual dimorphism and maturity (Taddei, 1999; Mansur *et al*., 2005; Lima *et al*., 2013; Silva *et al*., 2014), and condition factors (Araújo *et al*., 2012; Santos-Filho *et al*., 2016).

The power model determined the equations with the best fit. Because this model normally determines relationships with good predictive powers, it is among the most used for estimations of biomass of aquatic invertebrates, including insects (Smock, 1980; Meyer, 1989; Burgherr & Meyer, 1997; Miserandino, 2001) and freshwater crustaceans (Atar & Seçer, 2003; Branco & Fracasso, 2004; Lima *et al*., 2013). According to Wenzel *et al*. (1990), the differences observed in size-mass relationships determined by different mathematical models are generally small and tend to decrease with the number of observations. However, the use of different mathematical models to determine the equation with the best fit is strongly recommended (Wenzel *et al*., 1990; González *et al*., 2002), because a single model may not determine the best relationship for different body variables (Brito *et al*., 2015; Kiffer *et al*., 2016).

The wide variance found in the values of biomass and body variables indicated that specimens of different sizes were sampled in the two streams. According to Begon *et al*. (1996), this variation is important when determining size-mass relationships because it guarantees a better representation of the population logistic growth curve. In addition, the complete sclerotization of the body of crustaceans also contributes to the predictive power of the equations, because this characteristic promotes low variation in biomass among individuals of similar sizes (Benke *et al*., 1999).

Studies on species of the order Brachyura have demonstrated differences in the growth and size of individuals of different sexes (Pinheiro & Taddei, 2005; Taddei & Herrera, 2010; Marochi *et al*., 2016). In Brazil, these differences were also observed for the family Trichodactylidae, while Alarcon *et al*. (2002) found that males of *T. fluviatilis* were larger than females in the southeast; Zimmermann *et al*. (2009) and Silva *et al*. (2014) observed the opposite pattern in populations of *Trichodactylus panoplus* von Martens, 1869 located at the southern and northeastern regions, respectively. In the present study, the values of biomass, carapace length and width of the two populations did not differ between the sexes, although the coefficients of variation of these variables were higher in males. When assessing the relative growth and size of *T. fluviatilis*, Lima *et al*. (2013) also found no differences between males and females. Santos-Filho *et al*. (2016) observed similar values in males and females of this species and suggested that the sexual maturation of *T. fluviatilis* occurs in the same period for both sexes. Similar patterns have been observed in other species of the family Trichodactylidae (see Mansur *et al*., 2005 for *Dilocarcinus pagei* Stimpson, 1861; Venâncio & Leme, 2010 for *Trichodactylus petropolitanus* Goldi, 1886).

As expected, differences in size-mass relationships were found between the populations studied. For immature aquatic insects, some authors have observed that populations of the same species located in different geographic regions may determine different size-mass relationships (Smock, 1980; Meyer, 1989; Wenzel *et al*., 1990; Burgherr & Meyer, 1997). Part of this variation among populations can be explained by differences in the abiotic characteristics of the environment and by trophic or genetic conditions (González *et al*., 2002; Martins *et al*., 2014). Therefore, our results demonstrate that this variation can also occur in freshwater crustaceans. The estimation of biomass through size-mass relationships previously determined for different populations should be considered after cross-validation tests that evaluate the feasibility of their use (see Martins *et al*., 2014).

In linear models, the values of coefficient "*b*" on size-mass equations represent the rate of biomass increase with body size (Becker *et al*., 2009), which may be isometric ($b = 3$, weight, carapace length and width grow in equal proportions), negative allometric ($b < 3$, weight increases less in proportion to carapace length and width) and positive allometric ($b > 3$, weight increases more in proportion to carapace length and width; Santos-Filho *et al*., 2016). The equations determined for *T. fluviatilis* indicated a negative allometric growth pattern and were within the established range for other freshwater invertebrates (Cressa, 1999; Pinheiro & Taddei, 2005; Méthot *et al*., 2012). However, Benke *et al*. (1999) observed values of coefficient "*b*" that were higher than 3 in decapods in North America and suggested that the growth of chelipeds would be faster than the growth of the carapace. Our results showed that the biomass of *T. fluviatilis* seems to be more influenced by the body surface and external morphology of the carapace than volume (Wenzel *et al*., 1990; Towers *et al*., 1994).

In summary, the relationships determined in our study corroborated the use of carapace length and width as predictors of the biomass of *T. fluviatilis*. Furthermore, because no differences were observed in the models determined for males and females in the two populations studied, one single size-mass relationship can be used for individuals of both sexes. However, the differences found in the equations determined for the populations sampled in Macuco and Mestre Álvaro support the specificity of these relationships and the need for determining one equation for each population studied. Because of the scarcity of information about the biology of freshwater crustaceans in streams of the Atlantic Forest, the estimation of the biomass of *T. fluviatilis* through size-mass relationships constitutes an important contribution to the evaluation of the functional role of these macroconsumers in the detritus-based food webs of these ecosystems.

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Table 1. Ranges, means, standard deviations (SD) and coefficient of variations (CV, in percentage) for body variables (carapace length [CL], carapace width [CW], in cm) and dry mass (DM, in g) of individuals of *Trichodactylus fluviatilis* sampled in the Macuco and Mestre Álvaro streams. The data set was divided into 3 blocks: males, females and both sexes together. n = 45 (Macuco Stream) and 50 (Mestre Álvaro Stream). CV = (SD/mean) × 100.

Populations	Blocks	Variables	Range	Mean	SD	CV
Macuco	Males	CL	0.98 - 3.01	2.19	0.52	24.19
		CW	0.86 - 2.75	1.98	0.47	23.85
		DM	0.25 - 6.07	2.33	1.39	59.77
	Females	CL	1.57 - 2.59	1.94	0.25	12.88
		CW	1.55 - 2.41	1.81	0.23	13.13
		DM	0.88 - 3.41	1.50	0.60	40.48
	Both sexes	CL	0.86 - 2.75	1.93	0.41	21.70
		CW	0.98 - 3.01	2.11	0.47	22.34
		DM	0.25 - 6.07	2.07	1.26	60.74
Mestre Álvaro	Males	CL	0.30 - 2.80	1.91	0.61	31.72
		CW	0.40 - 3.20	2.08	0.68	32.50
		DM	0.03 - 8.42	2.67	1.88	70.49
	Females	CL	1.60 - 3.00	2.26	0.44	19.57
		CW	1.80 - 3.30	2.39	0.44	18.58
		DM	1.34 - 6.07	2.95	1.45	49.12
	Both sexes	CL	0.30 - 3.00	2.01	0.58	29.01
		CW	0.40 - 3.30	2.17	0.63	29.13
		DM	0.03 - 8.42	2.75	1.76	64.10

Table 2. Differences in the body variables and dry mass of *Trichodactylus fluviatilis* across the sexes and populations studied (Macuco and Mestre Álvaro) tested by Kruskal–Wallis tests. n = 45 (Macuco Stream) and 50 (Mestre Álvaro Stream). Degrees of freedom = 1.

Variables	**Sex**				**Populations**	
	Macuco		**Mestre Álvaro**			
	H	*p*	*H*	*p*	*H*	*p*
Carapace length	2.16	0.141	2.91	0.088	1.23	0.268
Carapace width	3.07	0.080	1.57	0.210	1.00	0.318
Dry mass	2.90	0.088	0.34	0.560	3.12	0.114

Table 3. Parameters (with 95% confidence intervals) of linear, exponential and power models for the relationship between linear body dimension (L = carapace length [CL], carapace width [CW], in cm) and dry mass (DM, g) of individuals of *Trichodactylus fluviatilis* sampled in the Macuco and Mestre Álvaro streams. The data set was divided into 3 blocks: males, females and both sexes together. a/b = regression coefficients, r^2 = coefficient of determination (*p < 0.001). n = 45 (Macuco Stream) and 50 (Mestre Álvaro Stream).

Function	Conversion	Blocks	Macuco stream				Mestre Álvaro stream			
			A	Ln a	B	r^2	a	Ln a	b	r^2
Linear										
DM = $a + b \cdot L$	CL → DM	Males	-2.86 ± 0.51		2.62 ± 0.25	0.79*	-2.61 ± 0.48		2.76 ± 0.24	0.79*
		Females	-2.32 ± 0.76		2.10 ± 0.41	0.68*	-3.99 ± 0.75		3.06 ± 0.32	0.88*
		Both	-3.05 ± 0.42		2.65 ± 0.21	0.77*	-2.60 ± 0.43		2.66 ± 0.20	0.77*
	CW → DM	Males	-2.82 ± 0.49		2.35 ± 0.22	0.80*	-2.37 ± 0.51		2.42 ± 0.23	0.76*
		Females	-2.58 ± 0.68		2.10 ± 0.35	0.75*	-4.42 ± 0.74		3.08 ± 0.30	0.89*
		Both	-2.98 ± 0.39		2.39 ± 0.18	0.80*	-2.52 ± 0.44		2.43 ± 0.19	0.76*
Exponential										
ln DM = ln $a + b \cdot L$	CL → DM	Males		-1.05 ± 0.08	0.66 ± 0.04	0.89*		-1.28 ± 0.09	0.79 ± 0.04	0.89*
		Females		-0.72 ± 0.17	0.48 ± 0.09	0.68*		-0.60 ± 0.11	0.45 ± 0.04	0.87*
		Both		-1.02 ± 0.07	0.65 ± 0.03	0.87*		-1.15 ± 0.08	0.72 ± 0.04	0.86*
	CW → DM	Males		-1.02 ± 0.09	0.59 ± 0.04	0.88*		-1.22 ± 0.10	0.70 ± 0.04	0.86*
		Females		-0.75 ± 0.15	0.48 ± 0.07	0.75*		-0.65 ± 0.12	-0.44 ± 0.05	0.87*
		Both		-0.98 ± 0.07	0.57 ± 0.03	0.87*		-1.14 ± 0.08	0.66 ± 0.03	0.85*
Power										
ln DM = ln $a + b \cdot \ln L$	CL → DM	Males		-0.48 ± 0.04	2.66 ± 0.15	0.91*		-0.40 ± 0.03	2.61 ± 0.09	0.95*
		Females		-0.38 ± 0.11	2.10 ± 0.42	0.67*		-0.39 ± 0.09	2.33 ± 0.26	0.87*
		Both		-0.49 ± 0.04	2.64 ± 0.14	0.89*		-0.41 ± 0.02	2.54 ± 0.08	0.94*
	CW → DM	Males		-0.60 ± 0.05	2.67 ± 0.15	0.91*		-0.50 ± 0.03	2.63 ± 0.10	0.94*
		Females		-0.47 ± 0.11	2.20 ± 0.39	0.72*		-0.53 ± 0.09	2.57 ± 0.26	0.89*
		Both		-0.54 ± 0.04	2.32 ± 0.06	0.90*		-0.46 ± 0.03	2.29 ± 0.04	0.94*

Table 4. Differences in the slopes of size-mass equations for *Trichodactylus fluviatilis* determined with the power model for carapace length and width across the sexes and populations studied (Macuco and Mestre Álvaro) tested by analysis of covariance (ANCOVA). n = 45 (Macuco Stream) and 50 (Mestre Álvaro Stream). SS = sum of squares. Degrees of freedom = 1.

Body variables	**Sexes**						**Populations**		
	Macuco			**Mestre Álvaro**					
	SS	*F*	*p*	SS	*F*	*p*	SS	*F*	*p*
Carapace length	0.00	0.66	0.421	0.09	3.29	0.076	0.07	6.94	0.010
Carapace width	0.01	1.43	0.239	0.07	2.65	0.110	0.11	10.73	0.001

Figure legend

Figure 1. Scatter diagrams of dry mass versus carapace length and width for individuals of *Trichodactylus fluviatilis* sampled in the Macuco (A, B) and Mestre Álvaro (C, D) streams on linear (squares; ■ = males and □ = females) and on logarithmic scales (circles; ● = males and ○ = females). The regression equations are power based for both populations: DM = $a \cdot L^b$ (in linear form: $\ln \mathrm{DM} = \ln a + b \cdot \ln L$).

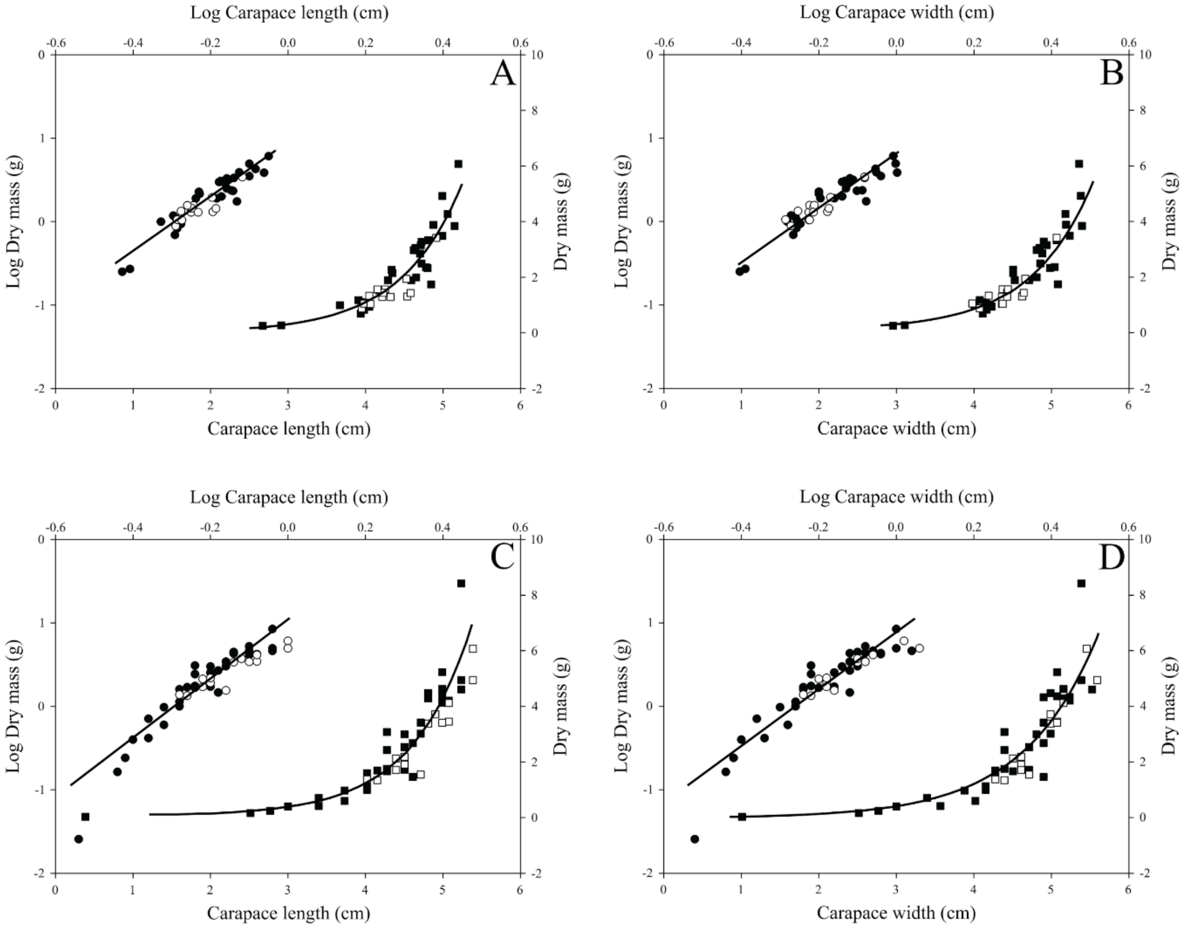
Log Carapace length (cm)
Log Carapace width (cm)
A
B
C
D
Log Dry mass (g)
Dry mass (g)
Carapace length (cm)
Carapace width (cm)
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0
1
2
3
4
5
6
-2
-1
8
10

Figure 1.

CAPÍTULO 2

Influence of *Trichodactylus fluviatilis* on leaf breakdown in streams: understanding the role of freshwater crabs in detritus-based food webs

Larissa Corteletti da Costa, Walace Pandolpho Kiffer Junior, Cinthia Gabriela Medeiros,
Juliana Rangel & Marcelo S. Moretti

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Influence of *Trichodactylus fluviatilis* on Leaf Breakdown in Streams: Understanding the Role of Freshwater Crabs in Detritus-based Food Webs

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Larissa Costa, Walace Kiffer Jr., Cinthia Casotti, Juliana Rangel, and Marcelo Moretti (2016) Freshwater crabs can affect leaf breakdown by consuming leaves or invertebrate shredders. The aims of this study were to analyze the gut content of *Trichodactylus fluviatilis* and evaluate the influence of this macroconsumer on leaf breakdown. For this, we (i) performed gut analyses of 55 individuals of *T. fluviatilis* and (ii) determined leaf decay rates and FPOM production in laboratory trials containing crabs and the caddisfly shredder *Triplectides* sp., alone and together, and leaves differing in quality. We hypothesized that *T. fluviatilis* feeds both on leaves and *Triplectides* sp. and, consequently, leaf decay rates would be lower when these organisms were together. The main food categories in *T. fluviatilis* guts were algae and FPOM, while CPOM and animal tissue were rare. Leaf decay rates and FPOM production did not differ across shredder treatments or leaf species. However, the survival of *Triplectides* sp. was higher when alone. The results support the potential for participation of *T. fluviatilis* in leaf breakdown and demonstrated that, in spite of the high abundances of algae and FPOM in the gut content, adults of this species have the potential to feed both on leaf litter and larvae of *Triplectides* sp. However, the hypothesis of this study was only partially corroborated because decay rates did not change across treatments.

Key words: Macroconsumers, Invertebrate shredders, Gut content analysis, Detritus chain, Atlantic Forest streams.

BACKGROUND

Forest headwater streams are heterotrophic ecosystems that depend on the inputs of allochthonous organic matter (Minshall 1967). In such streams, invertebrate shredders play an important role in the detritus-based food webs, converting leaf litter into fine particles of organic matter that will become available to other consumers (Graça 2001). Several studies have demonstrated that the feeding activity of shredders is affected by litter quality; *i.e.*, leaves with high nutrient content and low amounts of chemical and structural compounds are preferred (Rincón and Martínez 2006; Bastian et al. 2007; Casotti et al. 2014).

Immature stages of some Trichoptera, Plecoptera and Diptera are usually the main shredders in streams (Webster et al. 1999; Thompson and Townsend 2000). However, in tropical streams the abundance of this functional feeding group varies in different regions (see Boyero et al. 2009; Boyero et al. 2015; Graça et al. 2015) and macroconsumers, such as crabs and shrimps, can also shred leaf litter (Moulton et al. 2010; Williner and Collins 2013). Thus, the role of macroconsumers might have been overlooked in some studies evaluating leaf breakdown in tropical

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*Correspondence: E-mail: marcelo.moretti@uvv.br streams (Boyero et al. 2009) because of their high mobility, nocturnal activity and large size, which restrict their access to coarse meshes in leaf litter experiments. They are also difficult to observe and sample (Baumart et al. 2015). Additionally, by consuming different food categories, the trophic level of these organisms might have been wrongly assigned (Cheshire et al. 2005).

Considering their generalist feeding behavior, macroconsumers can influence leaf breakdown both positively, shredding leaf litter (Mancinelli et al. 2013), and negatively, preying on insect shredders (Williner and Collins 2013). In some ecosystems, the shredding capacity of macroconsumers may be equivalent to that of insect shredders (March et al. 2001). Because of their high biomass and activity, it is expected that macroconsumers may play an important role in leaf breakdown (Moss 2004). In addition, the predation pressure exerted by these organisms can affect the structure of aquatic invertebrates by modifying the abundance of some taxa (Silveira and Moulton 2000; Landeiro et al. 2008). If the abundance of insect shredders is reduced by macroconsumer predation, leaf decay rates could be reduced (Obernborfer et al. 1984).

The feeding ecology of macroconsumers in streams has been evaluated elsewhere (*e.g.*, Tomanova et al. 2006; Moulton et al. 2010; Masese et al. 2014) and different patterns have been observed. Kensely and Walker (1982) suggested that the shredding activity of shrimps of the genus *Macrobrachium* Bate, 1868 was accidental, resulting from their foraging strategy for obtaining fungal hyphae and larvae of mining chironomids. Landeiro et al. (2008) observed that the presence of these shrimps influenced the abundance of aquatic invertebrates more than leaf decay rates. On the other hand, Crowl et al. (2001) and Williner et al. (2014) observed a positive effect of shrimps and crabs on leaf breakdown; *i.e.*, leaf mass loss was higher in the presence of these organisms.

Freshwater crabs are considered omnivores (Obernborfer et al. 1984; Tomanova et al. 2006) and are abundant in Atlantic Forest streams (Moulton et al. 2010). In those ecosystems, the caddisfly shredder *Triplectides* Kolenati, 1859 (Trichoptera, Leptoceridae) is also abundant (Casotti et al. 2014; Kiffer et al. 2016). Given these organisms are frequently found associated with leaf patches, the aims of this study were to analyze the gut content of the crab *Trichodactylus fluviatilis* Latreille, 1828 (Brachyura, Trichodactylidae) and evaluate the influence of this macroconsumer on leaf breakdown. For this, we (i) performed gut analyses of individuals of *T. fluviatilis* sampled over one year and (ii) determined leaf decay rates and the production of fine particulate organic matter (FPOM) in laboratory trials containing individuals of *T. fluviatilis* and *Triplectides* sp., alone and together, and leaves differing in quality (*Miconia chartacea* Triana [Melastomataceae] and *Hoffmannia dusenii* Standley [Rubiaceae]). The survivorship of individuals of *Triplectides* sp. was also determined in trials where they were present. We hypothesized that *T. fluviatilis* feeds both on leaves and larvae of *Triplectides* sp. and, consequently, leaf decay rates would be lower when these organisms were together, given the presence of crabs would decrease the activity and abundance of insect shredders.

MATERIALS AND METHODS

Study area

Leaves and specimens of *T. fluviatilis* and *Triplectides* sp. were collected from Macuco Stream (20°01'23.8"S, 40°33'00.55"W; 593 m a.s.l.), in an Atlantic Forest fragment located in the State of Espírito Santo, SE Brazil. In this reach, the riparian vegetation was well-developed, shading approximately 80% of the streambed. The substrate was heterogeneous, composed of pebbles, gravel and leaf patches in pool areas. See Casotti et al. (2014) for additional physical and chemical information.

Gut content analysis

From July 2012 to June 2013, five adult specimens of *T. fluviatilis* were sampled monthly, except in May and June when only 2 and 3 individuals were found with the same sampling effort (three person-hours). The individuals were sexed (sex ratio; 1.2: 1), measured (carapace length; males: 1.91 ± 0.10 cm, females: 2.26 ± 0.12 cm) and fixed in formalin. In the laboratory, gut content analysis was performed according to Acosta and Prat (2011). The gut of each individual was removed and the full content spread over a gridded Sedgewick-Rafter counting cell (1 mm^2) containing a drop of glycerin and analyzed on a biological microscope (Opticam O400 Standard, 400x). The evaluation of the gut content was conducted by counting the occupied grids and determining the relative abundances of four pre-determined food categories: coarse particulate organic matter (CPOM, > 1 mm, including vascular plant tissue), fine particulate organic matter (FPOM, < 1 mm), algae (including unicellular and filamentous green algae and diatoms) and animal tissue (parts of prey exoskeleton). No mineral material was found in any gut ($n = 55$).

Laboratory trials

The influence of *T. fluviatilis* on leaf breakdown was evaluated in the laboratory using leaves of *M. chartacea* and *H. dusenii*, which are among the most abundant of the vertical inputs of leaf litter measured over a year in the Macuco Stream and are palatable to insect shredders (W. Kiffer, *pers. obs.*). These leaves were chosen because they differed in the content of nutrients and toughness; the lignin: N ratio was higher in *M. chartacea* than in *H. dusenii* (see Table 1). Leaves were collected with litter traps (1 m^2, 10 mm mesh) that were positioned 1.5 m above the ground along both stream banks. The nets were checked regularly, and senescent leaves were taken to the laboratory where they were air-dried and stored. Before the beginning of the experiment, leaves of both species were individually enclosed in litter bags (0.5 mm mesh) and conditioned for 15 days in the studied stream.

A total of 20 adult specimens of *T. fluviatilis* and 180 larvae of *Triplectides* sp. (2nd – 3rd instars) were collected manually in the Macuco Stream. Crabs and larvae were stored separately in coolers containing stream water, and taken to the laboratory, where they were starved at 21°C for 24 h under constant aeration and a 12: 12 h photoperiod.

Leaf decay rates and FPOM production were evaluated in three treatments containing leaves of both species and (i) one *T. fluviatilis*, (ii) nine *Triplectides* sp., and (iii) one *T. fluviatilis* and nine *Triplectides* sp. The number of individuals in treatments was based on the abundance ratio of *T. fluviatilis*: *Triplectides* sp. in the studied stream (1: 9), which was determined from monthly samplings of leaf patches over a year (4 samples per month). The initial dry mass of crabs (3.15 ± 0.25 g) and larvae (2.05 ± 0.12 mg) used in the experiment was determined from size-mass equations described for the studied populations using, respectively, the carapace length (L. Costa, unpublished data) and head capsule width (Kiffer et al. 2016) as predictors. These values did not differ between treatments (crabs: $t_{19} = -1.93$, $p = 0.069$; larvae: $t_{179} = 1.34$, $p = 0.183$).

Conditioned leaves of both species were cut into square pieces with approximately 5 cm wide. An initial wet mass of 1.00 ± 0.05 g, corresponding to 3-4 leaf pieces, of each species was placed randomly on the bottom of plastic boxes (30 × 35 × 13 cm; $n = 10$ per treatment) with 500 ml of filtered stream water. These leaves were offered together to evaluate if *T. fluviatilis* and *Triplectides* sp. would process leaves differing in quality differently. Ten additional replicates, containing leaves only, were used as controls to determine the mass loss of each leaf species in the absence of consumers. Conditioned leaves of both species were also used for the determination of correction factors dry mass/wet mass and calculate the initial dry mass of leaves. The feeding trials lasted for 10 days, under constant temperature (21°C), photoperiod (12: 12 h) and aeration. The replicates were monitored daily and the number of living larvae was recorded. At the end of the experiment, the remaining leaves of each species were removed with a pincer, dried (60°C, 72 h) and weighed (± 0.01 mg) separately. The water of each box was filtered over pre-weighed glass fiber filters (GF- 3, 0.6 µm, 47 mm, Macherey-Nagel, Germany) and the filters were dried (60°C, 72 h) and ashed (500°C, 4 h) for ash free dry mass (AFDM) determination of accumulated MOPF. In these trials, FPOM consisted of all organic particles that were produced by the shredding activity

Table 1. Nutrients, lignin and cellulose, and leaf toughness values of *M. chartacea* and *H. dusenii* leaves conditioned for 15 days. Leaf toughness was measured as the weight required to tear apart a leaf sample. Comparisons by *t*-tests (mean ± SE, *n* = 4)

	Nitrogen (%)	Phosphorus (%)	Lignin (%)	Cellulose (%)	Toughness (g)
M. chartacea	1.59 ± 0.04	0.050 ± 0.001	24.81 ± 4.83	21.29 ± 6.10	142.68 ± 21.49
H. dusenii	3.04 ± 0.03	0.024 ± 0.003	11.89 ± 0.24	24.55 ± 0.90	60.41 ± 28.49
T	56.73	-18.12	-5.35	1.06	-4.61
P	< 0.001	< 0.001	0.012	0.365	0.004

of consumers, regardless of whether they had passed through the shredders guts (feces) or not. Leaf final dry mass in each replicate was corrected using the mean dry mass of each species in the control replicates. To evaluate the potential of *T. fluviatilis* to feed both on leaves and larvae of *Triplectides* sp., the guts of all specimens used in the laboratory trials were analyzed as described previously.

Leaf analysis

Some conditioned leaves of both species were dried (60°C, 72 h), ground and homogenized for analyses of total N and P, lignin and cellulose (Graça et al. 2005). Leaf toughness was estimated using a tearing device built in the laboratory with simple materials that measures the force needed to tear apart a leaf sample (see Graça and Zimmer 2005). The characteristics of the studied leaves are presented in Table 1.

Data analysis

Because the relative abundances of food categories found in the guts of *T. fluviatilis* did not differ across sampling months and sexes (Kruskal-Wallis, $p > 0.05$), data were grouped and abundances of the food categories were compared by Friedman test, a non-parametric test for equality of medians in several repeated-measures univariate groups (Hammer et al. 2001). Paired Wilcoxon tests were used for *post hoc* comparisons. Leaf decay rates (k, day^{-1}) were estimated from the exponential model $M_f / M_i = e^{-kt}$, where M_f and M_i are the final and initial dry mass and t = 10 days (Olson 1963). General linear models (GLMs) were used to compare the decay rates and amounts of FPOM produced across shredder treatments and leaf species. Data of FPOM production was transformed (ln [x + 1]) to meet the assumptions of normality and homoscedasticity. When a model was significant, Tukey tests were used for *post hoc* comparisons. *Triplectides* sp. survival proportions in the presence and absence of crabs were compared by *t*-test. All statistical analyses were performed in PAST (version 3.8, University of Oslo) and SPSS (version 23.0 for Macintosh, SPSS, Chicago, Illinois), according to Zar (2010).

RESULTS

The main food categories in *T. fluviatilis* guts were algae and FPOM; CPOM and animal tissue were rare and together accounted for less than 2% of the content of analyzed guts (Friedman test: $X^2 = 145.52$, $p < 0.001$; Wilcoxon tests; Fig. 1).

In the laboratory trials, leaf decay rates (-*k*) ranged from 0.057 ± 0.008 to 0.090 ± 0.019 day^{-1} (Fig. 2). The decay rates of leaves of *M. chartacea* were similar across shredder treatments, while the decay rates of *H. dusenii* had more variation and were lower in the treatment containing *T. fluviatilis* only. However, the observed leaf decay rates did not differ significantly across treatments or leaf species (Table 2). The amounts of FPOM produced ranged from 20.50 ± 8.42 to 28.84 ± 12.50 mg, with no differences among treatments ($F_{2,29} = 0.09$, $p = 0.905$; Fig. 3). After 10 days, the survivorship

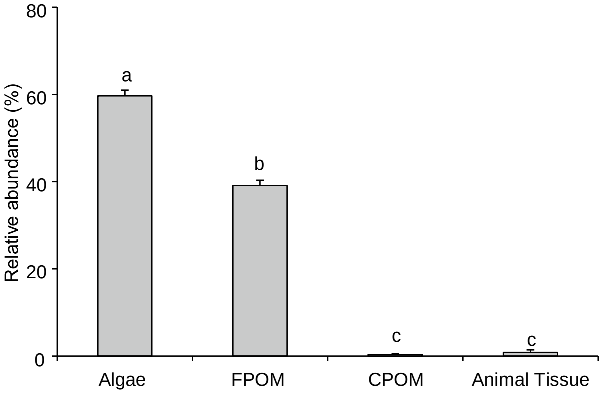

Fig. 1. Relative abundance (mean ± SE) of food categories in the gut contents of *T. fluviatilis*. Abundances with the same letter do not differ significantly (*post hoc* tests by simple pairwise Wilcoxon; *n* = 55).

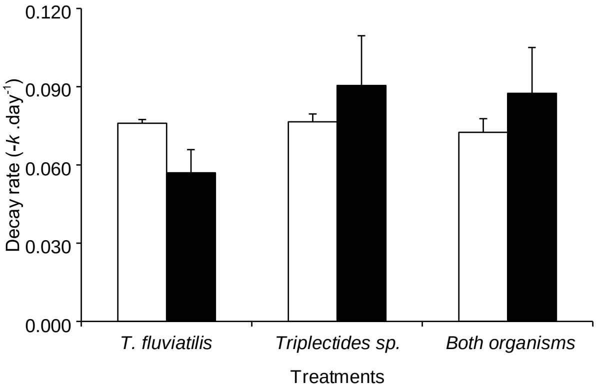

Fig. 2. Leaf decay rates (mean ± SE) of *M. chartacea* (empty bars) and *H. dusenii* (solid bars) leaves in treatments containing *T. fluviatilis* and *Triplectides* sp., alone and together

of *Triplectides* sp. was higher when alone (84 ± 4 %) than when *T. fluviatilis* was present (46 ± 8 %; $t_{19} = 3.54$, $p < 0.001$). MOPF was the main food category in the guts of specimens of *T. fluviatilis* used in the laboratory trials; CPOM was rare and accounted for less than 0.2% (Table 3). Animal tissue was only found in trials containing both organisms, but the relative abundance of this food category did not differ from CPOM.

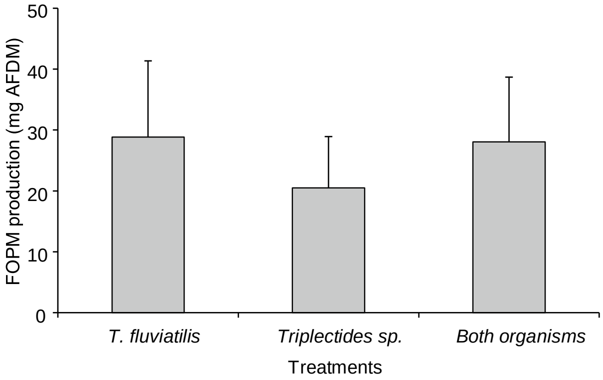

Fig. 3. Total amounts (mean ± SE) of MOPF produced in treatments containing *T. fluviatilis* and *Triplectides* sp., alone and together. AFDM = ash free dry mass.

DISCUSSION

Algae were the most abundant food category in the guts of *T. fluviatilis*. Algae have a high nutritional value (Lieske and Zwick 2007; Deegan and Ganf 2008; Leberfinger and Bohman 2010), especially when compared to leaf litter (Cushing and Allan 2001; Yoshimura et al. 2008). A large part of algal biomass consists of carbohydrates, proteins, lipids and other compounds essential to consumers (Sterner and Hesse 1994). Cummings and Klug (1979) suggested that some taxa of aquatic invertebrates might depend on the primary production of algae and macrophytes, even in streams where light availability is limited by the riparian vegetation.

Trichodactylid crabs have a wide trophic spectrum and may consume algae, plant tissue, leaf litter, aquatic invertebrates and even small vertebrates (Collins et al. 2007; Williner et al. 2014). The low abundances of CPOM found in the gut content of *T. fluviatilis*, even in the specimens used in the laboratory trials that fed on leaves, suggest that the particles of organic matter reach the guts at small sizes; *i.e.*, in the form of MOPF. The stomach of decapods has a muscular and nervous complex in which a set of striated muscles moves the skeletal elements of

Table 2. Variation in leaf decay rates depending on shredders (*T. fluviatilis*, *Triplectides* sp. and both together) and leaf species (*M. chartacea* and *H. dusenii*) tested by general linear models

	SS	*d.f.*	*F*	*p*
Leaf decay rates				
Shredders	0.0032	2	1.229	0.301
Leaf species	0.0001	1	0.126	0.724
Interaction	0.0037	2	1.417	0.251
Error	0.0709	54		

SS: sum of squares, df: degrees of freedom.

Table 3. Relative abundance of food categories in the guts of specimens of *T. fluviatilis* used in the laboratory trials, alone and together with *Triplectides* sp. Comparisons by Friedman test. Abundances with the same letter do not differ significantly (*post hoc* tests by simple pairwise Wilcoxon; mean ± SE, *n* = 10 per treatment)

	T. fluviatilis	Both organisms
MOPF	99.85 ± 0.28^a	94.07 ± 3.11^a
CPOM	0.15 ± 0.10^b	0.10 ± 0.07^b
Animal Tissue	–	5.83 ± 3.13^b
X^2	9.42	17.37
p	0.003	< 0.001

the gastric mill (Meiss and Norman 1977). Alves et al. (2010) showed the ossicles of this structure are well developed and calcified in adults of the family Trichodactylidae. Therefore, the foregut of *T. fluviatilis* can break and grind the ingested food, resulting in the low amounts of CPOM observed in the analyzed guts. On the other hand, the low abundance of animal tissue suggests that adults of *T. fluviatilis* do not exert a significant predation pressure on aquatic invertebrate communities associated with leaf patches. Normally, in the gut content of crustaceans, only the most keratinized parts of the exoskeletons of their prey are found, such as legs and head capsules (Acosta and Prat 2011). In our study, the parts of exoskeleton found in the guts were so rare and fine ground that we could not identify them taxonomically.

Given that larvae of insect shredders have a preference for feeding on high quality leaves, *i.e.*, those with low C: N and lignin: N ratios (Casotti et al. 2014; Leite-Rossi et al. 2016; Graça et al. 2016), we expected that *H. dusenii* would be more processed and, consequently, the decay rates would differ between leaf species at least in the treatment containing *Triplectides* sp. only. However, *T. fluviatilis* and *Triplectides* sp. processed similar amounts of leaves across all treatments, suggesting that differences in the characteristics of studied leaves were not sufficient to differentiate the activity of these organisms. When compared to other species from the tropical region, leaves of the Atlantic Forest are generally softer and have higher nutritional quality (see Graça and Cressa 2010; Graça et al. 2015). The high N content observed in both leaves, which is an important driver in leaf consumption by aquatic invertebrates (Leroy and Marks 2006; Graça and Cressa 2010), may have promoted the shredding activity in such way that consumers exhibited no preference for any species. Because of the mouthpart structure, which has prehensile appendages (mandibles and maxillae; Ceccaldi 1989), freshwater crabs could be more adapted to ingest tough leaves than typical aquatic insect shredders. If freshwater crabs have the ability to consume a wide range of leaf species and unconditioned leaves, as was observed for their counterparts from land and mangrove habitats (Kristensen et al. 2010; Nordhaus et al. 2011), these consumers may feed on leaves that are not preferred by shredders. In this context, leaf processing by macroconsumers may be more relevant in streams where shredders are scarce (Moulton et al. 2010). However, the ability of macroconsumers to process leaves of poor quality, which are typically refractory to many insect shredders (Li and Dudgeon 2008; Jabiol and Chauvet 2012), should be better evaluated.

Contrasting with the abundances of food categories in the guts of *T. fluviatilis* in the wild, *Triplectides* sp. survival was lower in the presence of crabs. In trials containing both organisms, we observed that some cases of *Triplectides* sp. were drilled and found with no larva inside. In addition, a significant abundance of animal tissue was recorded in the guts of the crabs used in the mixed treatment (5.83 ± 3.13%; Table 3). Thus, our study confirmed the ability of these crabs to prey on insect shredders at least when confined together. Given larvae of *Triplectides* sp. are abundant in the studied stream (Casotti et al. 2014; Kiffer et al. 2016), the low proportion of animal tissue in the guts of *T. fluviatilis* associated with leaf patches possibly results from an efficient defensive strategy of aquatic invertebrates, such as camouflage with the substrate or different timing of activity (Williams et al. 1987; Camargos and Pes 2011), or a preference of crabs for other food categories. All of these hypotheses remain to be tested in future studies.

A reduction in the abundance of shredders caused by macroconsumer predation could alter leaf decay rates in streams (Usio 2000). Using the same abundance ratio of *T. fluviatilis*: *Triplectides* sp. observed *in situ* (1: 9), our results suggest that *T. fluviatilis* may contribute to leaf processing and its influence on leaf decay rates and MOPF production does not seem to differ from *Triplectides* sp. In addition, the high manipulation of leaves by crabs in the laboratory, *i.e.* the behavior of holding, rotating or moving leaves with the chelipeds, probably compensated for the effect of larvae that were lost in the mixed treatment. Freshwater crabs can significantly promote the decomposition of organic matter, reducing particle size during foraging (Landeiro et al. 2008) and removing the substrate (Moulton et al. 2010). However, because of the smaller size, larvae of *Triplectides* sp. process higher amounts of leaf litter per unit of biomass and may be more important to energy flow in streams where both organisms occur together (Boyero et al. 2006).

CONCLUSIONS

The obtained results support the potential for participation of *T. fluviatilis* in leaf breakdown and demonstrated that, in spite of the high abundances of algae and MOPF in the gut content of *T. fluviatilis* in the wild, adults of this species have the potential to feed both on leaf litter and larvae of *Triplectides* sp. However, the hypothesis of this study (that *T. fluviatilis* feeds both on leaves and *Triplectides* sp. and, consequently, leaf decay rates would be lower when these organisms were together) was only partially corroborated because decay rates did not change across treatments.

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CAPÍTULO 3

Capacidade de fragmentação e comportamento alimentar do macroconsumidor *Trichodactylus fluviatilis* (Decapoda, Trichodactylidae) em riachos de Mata Atlântica

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Capacidade de fragmentação e comportamento alimentar do macroconsumidor *Trichodactylus fluviatilis* (Decapoda, Trichodactylidae) em riachos de Mata Atlântica

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***Running title*:** Capacidade de fragmentação e comportamento alimentar de *T. fluviatilis*

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RESUMO

Crustáceos macroconsumidores e insetos fragmentadores são componentes importantes das cadeias tróficas em riachos florestados. O objetivo deste estudo foi avaliar a capacidade de fragmentação e o comportamento alimentar de *Trichodactylus fluviatilis* na presença de diferentes detritos foliares e insetos fragmentadores. Foi hipotetizado que a qualidade dos detritos influenciaria a capacidade de fragmentação dos caranguejos e que estes iriam preferir se alimentar dos insetos em relação aos detritos foliares. Dessa forma, foram oferecidos aos caranguejos detritos foliares que apresentam diferenças em suas características físicas e químicas (*Hoffmannia dusenii*, *Miconia chartacea*, *Myrcia lineata* e *Eucalyptus globulus*) e larvas de dois invertebrados fragmentadores que constroem abrigos com diferentes materiais (*Phylloicus major* e *Triplectides gracilis*). As taxas de fragmentação foram maiores no tratamento que continha *M. lineata*, espécie de maior dureza foliar. As taxas de produção de matéria orgânica particulada fina foram maiores nos tratamentos que continham *M. chartacea* e *H. dusenii* em relação a *E. globulus* e *M. lineata*. Quando os itens alimentares foram oferecidos em combinações pareadas, a frequência de observação dos caranguejos em um dos itens alimentares não diferiu de 50% em nenhum dos tratamentos, indicando que a escolha dos itens alimentares foi aleatória. No entanto, a predação das larvas de *P. major* por *T. fluviatilis* foi maior que a das larvas de *T. gracilis*. Os resultados obtidos indicam que *T. fluviatilis* fragmenta detritos de baixa qualidade, recursos que são muitas vezes rejeitados pelos insetos fragmentadores, e evidenciam sua importância no processamento de detritos foliares em ambientes aquáticos.

PALAVRAS-CHAVE: interações tróficas, crustáceo dulcícola, invertebrados fragmentadores, ambientes lóticos.

ABSTRACT

Crustaceans macroconsumers and shredders insects are important components of the trophic chains in forested streams. The objective of this study was to evaluate the fragmentation capacity and the feeding behavior of *Trichodactylus fluviatilis* when exposed to different leaf litter and shredders insects. It was hypothesized that the quality of the detritus would influence the fragmentation capacity of the crabs and that they would prefer to feed on the insects in relation to the foliar detritus. Thus, detritus was offered to crabs that exhibit differences in their physical and chemical characteristics (*Hoffmannia dusenii*, *Miconia chartacea*, *Myrcia lineata* and *Eucalyptus globulus*) and larvae of two shredders invertebrates that construct shelters with different materials (*Phylloicus major* and *Triplectides gracilis*). The fragmentation rates were higher in the treatment containing *M. lineata*, a species with higher leaf hardness. The rates of fine particulate organic matter production were higher in the treatments containing *M. chartacea* and *H. dusenii* in relation to *E. globulus* and *M. lineata*. When food items were offered in paired combinations, the frequency of observation of crabs in one of the food items did not differ by 50% in any of the treatments, indicating that the choice of food items was random. However, the predation of larvae of *P. major* by *T. fluviatilis* was higher than that of larvae of *T. gracilis*. The results indicate that *T. fluviatilis* fragments low quality detritus, which are often rejected by the shredders insects, and show its importance in the processing of foliar debris in aquatic environments.

KEY WORDS: Trophic interactions, feshwater crustaceans, shredder invertebrates, lotic environments.

INTRODUÇÃO

A decomposição de detritos foliares é um processo de grande importância em riachos de pequena ordem, pois fornece energia e matéria para os organismos heterotróficos em ecossistemas onde a produtividade primária é limitada pelo sombreamento causado pela vegetação ripária (Moretti *et al.,* 2007; Ligeiro *et al.,* 2010). Uma das fases mais importantes do processo de decomposição é a fragmentação biológica, realizada principalmente por invertebrados que transformam a matéria orgânica particulada grossa (MOPG) em matéria orgânica particulada fina (MOPF), que se tornará então disponível para os demais consumidores (Cheshire *et al.,* 2005).

No geral, os insetos são considerados os principais organismos fragmentadores em riachos florestados (Webster *et al*., 1999; Thompson & Townsend, 2000). Entretanto, estudos recentes demonstraram que organismos macroconsumidores (p. ex. caranguejos, camarões e peixes) podem também influenciar o processamento de detritos foliares em riachos tropicais (Moulton *et al*., 2010; Cogo & Santos, 2013; Williner & Collins, 2013; Mancinelli *et al.,* 2013; Costa *et al*., 2016). Contudo, o papel desses macroconsumidores no processamento de detritos foliares em ambientes lóticos pode ter sido negligenciado em alguns estudos (Boyero *et al.,* 2009), devido ao hábito noturno e à grande mobilidade destes organismos dificultarem a sua visualização e amostragem (Magalhães, 2003). Além disso, estes organismos podem ter sido classificados equivocadamente quanto ao seu nível trófico (Cheshire *et al*., 2005), contribuindo para a ausência de informações do papel dos macroconsumidores no processamento de detritos vegetais em riachos tropicais.

Crustáceos decápodas, como caranguejos e camarões, atuam em diferentes níveis tróficos, alimentando-se de algas, detritos vegetais, invertebrados e pequenos vertebrados (Cumberlidge *et al*., 2009; Burress *et al*., 2013; Costa *et al*., 2016). Esses organismos são conhecidos por serem engenheiros ecológicos (Jones *et al*., 1994; Crowl *et al*., 2001; Moore, 2006), uma vez que influenciam na composição da comunidade e nos processos ecossistêmicos ocasionando profundos efeitos através da bioturbação, excreção e consumo de material vegetal e detritos (Crowl *et al*., 2001; Moulton *et al*., 2010; Brown & Lawson, 2010). Considerando seu comportamento alimentar generalista, esses macroconsumidores podem influenciar no processo de decomposição positivamente, fragmentando a matéria orgânica alóctone (Mancinelli *et al*., 2013), e negativamente, predando os invertebrados fragmentadores (Williner & Collins, 2013). Desta forma, representam um importante componente das teias tróficas aquáticas contribuindo para o balanço energético de pequenos riachos (Collins *et al*., 2006; Teodósio & Masunari, 2009; Williner *et al*., 2009).

No geral, a qualidade foliar é um fator importante no comportamento alimentar de invertebrados detritívoros, podendo influenciar o desempenho e a distribuição destes organismos (Iversen, 1974; Peckarsky, 1980; Irons *et al*., 1988; Nolen & Pearson, 1993; Ardón *et al*., 2006; Carvalho & Uieda, 2010; Casotti *et al.,* 2015; Kiffer *et al*., 2016). Algumas espécies de caranguejos podem apresentar preferência por determinados itens alimentares. No entanto, como nem sempre os itens de maior valor nutricional estão disponíveis no ambiente, a sobrevivência destes organismos depende da sua capacidade de explorar recursos de baixa qualidade (Mancinelli *et al*., 2013). Informações sobre a habilidade desses organismos em fragmentar, digerir e assimilar recursos de menor valor energético, como os detritos foliares, são cruciais para a compreensão do papel ecológico desses organismos nos ecossistemas aquáticos.

Os caranguejos exploram uma diversa gama de recursos alimentares, como algas, microrganismos e detritos orgânicos. No entanto, estes organismos podem complementar a sua dieta com tecido animal quando disponível no ambiente, sendo poucas espécies consideradas exclusivamente como carnívoras (Mancinelli *et al*., 2013). Estudos relacionados às interações predador-presa são focados, em sua maioria, nas cadeias tróficas que tem como base os produtores primários (Greig & McIntosh, 2006). Contudo, em pequenos riachos florestados, onde os detritos orgânicos de origem alóctone constituem a base das cadeias tróficas, as interações entre organismos detritívoros e seus predadores são raramente estudadas (Greig & McIntosh, 2006). Desta forma, estes ecossistemas heterotróficos podem ser alterados pelas interações entre os níveis tróficos do sistema decompositor, uma vez que os predadores podem afetar diretamente o processamento dos detritos orgânicos ao influenciar a densidade ou o comportamento alimentar de organismos detritívoros (Lawrence & Wise, 2000; Mancinelli *et al*., 2002).

Os insetos detritívoros, como as larvas das espécies *Triplectides gracilis*

(Burmeister, 1839) (Trichoptera, Leptoceridae) e *Phylloicus major* Müller, 1880 (Trichoptera, Calamoceratidae), e os caranguejos macroconsumidores da espécie *Trichodactylus fluviatilis* Latreille, 1828 (Decapoda, Trichodactylidae) são característicos de ecossistemas lóticos, e estão presentes em corpos hídricos com drenagem Atlântica (Casotti *et al*., 2015; Kiffer *et al.*, 2016; Costa *et al*., 2016). As larvas de Trichoptera são fragmentadoras de detritos orgânicos, utilizando estes recursos para construção de abrigos e alimentação (Williams *et al*., 1987; Anderson & Cummins, 1979; Otto, 2000). Costa *et al.* (2016) observaram que estes organismos são também utilizados como recurso alimentar por indivíduos de *T. fluviatilis*. Dada a coexistência e as interações tróficas observadas, estas espécies constituem um importante componente do processamento de detritos foliares nos riachos de Mata Atlântica (Becker *et al*., 2009; Boyero *et al*., 2011).

O objetivo deste estudo foi avaliar a capacidade de fragmentação e o comportamento alimentar de *T. fluviatilis* na presença de diferentes detritos foliares e insetos fragmentadores. Para isso, as taxas de processamento de detritos foliares foram determinadas quando os indivíduos se encontravam separadamente ao detritos de 4 espécies arbóreas (*Hoffmannia dusenii* Standl [Rubiacea], *Miconia chartacea* Triana [Melostamatacea], *Myrcia lineata* O. Berg [Myrtacea] e *Eucalyptus globulus* Labill [Myrtacea]) que apresentam diferentes características físicas e químicas. Além disso, o comportamento alimentar de *T. fluviatilis* foi avaliado quando os indivíduos foram à combinações pareadas de detritos foliares (*H. dusenii*, *M. chartacea*) e larvas de insetos fragmentadores que constroem abrigos com materiais diferentes (*Phylloicus major* Müller, 1880 [abrigos de folhas] e *Triplectides gracilis* Burmeister, 1839 [abrigos de gravetos]). Foi hipotetizado que a qualidade dos detritos influenciaria a capacidade de fragmentação dos caranguejos e que estes, iriam preferir se alimentar das larvas fragmentadoras em relação aos detritos foliares.

MATERIAIS E MÉTODOS

Coleta dos organismos

Os caranguejos e os insetos fragmentadores foram coletados no riacho Macuco (20º01’23.1” S, 40º32’58.6” W; 593 m). Este riacho encontra-se em um fragmento de Mata Atlântica e possui o substrato bastante heterogêneo, formado por cascalho, areia e grandes acúmulos de detritos foliares, onde estes organismos normalmente são encontrados.

Os indivíduos de *Trichodactylus fluviatilis* foram coletados utilizando dois procedimentos, a fim de potencializar a amostragem. Primeiramente, foi realizada a busca ativa dos indivíduos (2 pessoas por 2 h), a qual consistiu na sua procura direta, revirando seixos, acúmulos de detritos foliares e troncos submersos. Além disso, devido ao hábito noturno dos organismos, também foram utilizadas armadilhas do tipo “covo” contendo iscas (fígado de galinha), que permaneceram submersas no riacho por 24 h. Após a captura, os indivíduos foram acondicionados em uma caixa térmica contendo a água do próprio riacho sobre constante aeração e levados para o laboratório. Os caranguejos foram colocados individualmente em aquários (12 cm de diâmetro, 8 cm de altura) contendo 400 ml de água e detritos foliares do próprio riacho e mantidos por uma semana, sob temperatura (21º C), aeração e fotoperíodo (12 h: 12 h) constantes, para aclimatação. Previamente ao início dos experimentos, os indivíduos foram mantidos sem alimentação por 48 h.

As larvas de *Phylloicus major* e *Triplectides gracilis* são comumente visualizadas sobre os acúmulos de folhas formados nas áreas de remanso no riacho estudado. Os fragmentadores foram coletados manualmente, utilizando redes de mão. As larvas coletadas foram acondicionadas separadamente em caixas térmicas e transportadas e aclimatadas no laboratório conforme descrito anteriormente.

Detritos foliares

Detritos foliares de 04 espécies arbóreas foram utilizados nos experimentos, sendo 03 espécias nativas (*Hoffmannia dusenii*, *Miconia chartacea* e *Myrcia lineata*) e 01 exótica (*Eucaliptus. globulus*). As espécies nativas foram escolhidas por apresentarem diferenças em suas qualidades (boa: *H. dusenii*; intermediária: *M. chartacea*; e ruim: *M. lineata*), enquanto *E. globulus* foi utilizada por estar presente na zona ripária de alguns trechos do córrego Macuco (ver Capítulo 2). Os detritos destas espécies foram coletados mensalmente no córrego Macuco utilizando redes (1 m^2, 10 mm de malha) fixadas a aproximadamente 1,5 m do solo em ambas as margens do riacho. Os detritos retidos em cada rede foram transportados em sacos plásticos para o laboratório, secos à temperatura ambiente, triados e acondicionados em caixas plásticas. Previamente ao início dos experimentos, os detritos de cada espécie foram incubados separadamente em *litter bags* (15 x 20 cm) de malha fina (0,5 mm) por 15 dias no riacho estudado, para que ocorressem os processos de lixiviação e colonização microbiana (condicionamento).

Após a incubação, parte dos detritos de cada espécie foi seca (60º C, 72 h) para a determinação das características físicas e químicas. Discos de 14 mm de diâmetro foram cortados dos detritos com um cortador de cortiça para a determinação da dureza foliar (Graça & Zimmer, 2005). Os detritos foliares foram então moídos para a determinação das concentrações de nitrogênio (Flindt & Lillebo, 2005) e fósforo (Flindt & Lillebo, 2005). As concentrações de polifenóis foram determinadas através do método Folin-Denis (Bärlocher & Graça, 2005), e as de celulose e lignina foram determinadas por gravimetria (método de Goering & Van Soest, segundo Gessner, 2005). Todas as análises foram realizadas com 4 réplicas.

Capacidade de fragmentação de T. fluviatilis

Neste experimento, 40 indivíduos de *T. fluviatilis* foram separados em quatro tratamentos, sendo que em cada tratamento foram oferecidos detritos foliares condicionados de uma única espécie. Desta forma, nos aquários descritos acima, que continham 01 indivíduo de *T. fluviatilis* cada, 03 discos foliares (50 mm) condicionados da mesma espécie foram oferecidos. Os recipientes continham 600 ml de água do córrego filtrada e apresentavam fundo rugoso, para facilitar a locomoção dos caranguejos. Os aquários permaneceram aerados durante todo o experimento e 10 réplicas foram montadas para cada tratamento. Cinco réplicas adicionais, que continham apenas os discos foliares, foram montadas para cada tratamento para a determinação de perda de peso dos detritos de cada espécie na ausência de fragmentadores e correção das taxas de perda de peso dos discos no final do experimento. O experimento teve duração de 10 dias.

Após o término do experimento, os discos remanescentes e os organismos foram secos (60º C, 72 h) e pesados (0,1 mg) para a determinação do peso seco. Para a determinação das taxas de produção de matéria orgânica particulada fina (MOPF), a água dos recipientes foi filtrada em filtros GF/F pré-pesados. Os filtros foram então secos e pesados, conforme descrito anteriormente. As taxas de fragmentação e produção de MOPF foram expressas em termos de massa de material foliar (mg) perdida ou produzida por dia.

Comportamento alimentar de T. fluviatilis

Para este experimento, 60 indivíduos de *T. fluviatilis* foram utilizados. Como recurso alimentar para os caranguejos, foram utilizados detritos foliares de *H. dusenii* e *M. chartacae* e larvas de *T. gracilis* e *P. major*. Os detritos destas espécies foram escolhidos por apresentarem diferenças em suas características físicas e químicas enquanto os fragmentadores foram escolhidos por construírem abrigos com materiais diferentes. Os itens alimentares foram oferecidos para os crustáceos em todas as combinações pareadas possíveis: (i) *H. dusenii* e *M. chartacae*, (ii) *H. dusenii* e 03 larvas de *T. gracilis*, (iii) *H. dusenii* e 03 larvas de *P. major*, (iv) *M. chartacae* e 03 larvas de *T. gracilis*, (v) *M. chartacae* e 03 larvas de *P. major* e (vi) 03 larvas de *T. gracilis* e 03 larvas de *P. major*.

Os experimentos foram montados em aquários de acrílico com formato de “Y”. Estes aquários, continham um “degrau” em cada uma das duas extremidades mais próximas, onde o recurso alimentar, larvas ou folhas, permaneceu retido. Os detritos foliares foram oferecidos na forma de discos com 50 mm de diâmetro. Os aquários continham água do riacho filtrada e foram mantidos sobre as condições de temperatura, oxigenação e fotoperíodo descritos anteriormente. Dez réplicas foram montadas para cada tratamento (combinação pareada). O experimento teve duração de 6 horas, sendo que as réplicas de cada tratamento foram monitoradas a cada 1 hora para a determinação de qual extremidade do aquário (item alimentar) os caranguejos se encontravam.

Análise de dados

As diferenças nas características físicas e químicas dos detritos foliares estudados foram testadas por Análise de Variância (ANOVA). As taxas de fragmentação e produção de MOPF observadas no primeiro experimento também foram comparadas entre os tratamentos por ANOVA. Quando os modelos foram significativos, testes de Tukey foram realizados para comparações *a posteriori*. Todos os dados tiveram suas normalidades e homogeneidades de variância testadas.

Testes z de proporções foram utilizados para testar se um dos itens alimentares oferecidos aos caranguejos foi significativamente mais escolhido pelos caranguejos nos tratamentos do segundo experimento. Desta forma, as frequências de escolha dos caranguejos foram testadas nas seguintes combinações: larvas (*P. major* e *T. gracilis*) vs. detritos foliares (*M. chartacea* e *H. dusenii*); *M. chartacea* vs. *H. dusenii*; *P. major* vs. *T. gracilis*. As frequências dos indivíduos que inicialmente escolheram as larvas (*P. major* e *T. gracilis*) e posteriormente trocaram para detritos ou que escolheram inicialmente *P. major* e posteriormente trocaram para *T. gracilis* também foram testadas. As análises estatísticas foram realizadas utilizando-se o programa Statistica 7 (StatSoft Inc., Tulsa, USA), de acordo com Zar (2010).

RESULTADOS

Detritos foliares

Os detritos foliares das espécies estudadas apresentaram diferenças em suas características físicas e químicas (Tabela 1). Os detritos de *E. globulus* apresentaram os maiores teores de lignina (55,37 ± 0,37 %) e celulose (48,40 ± 2,37 %), enquanto os valores de dureza (201,86 ± 41,35 g) e compostos fenólicos (0,57 ± 0,007 %) foram intermediários. *M. chartacea* apresentou os menores teores de nitrogênio (1,41 ± 0,07 %) e valores intermediários de lignina (10,04 ± 1,15 %). Os detritos de *M. lineata* apresentaram os maiores valores de dureza (512,13 ± 33,48 g) e os menores teores de compostos fenólicos (0,11 ± 0,002 %). Enquanto os detritos de *H. dusenii* apresentaram os maiores teores de nitrogênio e fósforo (2,91 ± 0,02 % e 0,17 ± 0,0020 %, respectivamente) e os menores valores de dureza (60,91 ± 16,04 %) (Tabela 1).

Tabela 1. Características químicas e físicas dos detritos foliares das espécies utilizadas nos experimentos, após 21 dias de condicionamento no riacho Macuco, Santa Leopoldina (ES). A dureza foliar foi expressa como o peso necessário para romper um disco de folha. *F* e *P* indicam os resultados das ANOVAs. Letras diferentes indicam diferenças estatísticas entre as espécies vegetais. Média ± EP, n = 4. ML = *Myrcia lineata*; EG = *Eucalyptus globulus*; MC = *Miconia chartacea*; HD = *Hoffmannia dusenii*.

Detritos	Nitrogênio (%)	Fósforo (%)	Fenóis (%)	Lignina (%)	Celulose (%)	Dureza (g)
ML	1,44 ± 0,07^{c}	0,02 ± 0,005^{b}	011 ± 0,002^{d}	8,29 ± 0,61^{b}	2,62 ± 0,24^{b}	512,13 ± 33,48^{c}
EG	2,03 ± 0,04^{b}	0,09 ± 0,025^{b}	0,57 ± 0,007^{c}	55,37 ± 0,37^{a}	48,40 ± 2,37^{a}	201,86 ± 41,35^{b}
MC	1,41 ± 0,07^{c}	0,03 ± 0,008^{b}	0,88 ± 0,005^{b}	10,04 ± 1,15^{b}	3,43 ± 1,30^{b}	14268 ± 10.,74^{a}
HD	2,91 ± 0,02^{a}	0,17 ± 0,020^{a}	1,14 ± 0,031^{a}	5,28 ± 2,20^{b}	17,87 ± 2,23^{b}	60,91 ± 16,04^{a}
F	249,04	17,56	730,87	199,76	66,61	64,74
P	<0,001	0,001	<0,001	<0,001	<0,001	<0,001

Taxas fragmentação e produção de MOPF

As taxas de fragmentação de *T. fluviatilis* diferiram entre os tratamentos (F = 63,95, p < 0,01). As maiores taxas de fragmentação foram observadas no tratamento que continha discos de *M. lineata* (11,74 ± 0,45 mg.dia^{-1}), seguido por *M. chartacea* (7,50 ± 0,39 mg.dia^{-1}). Os tratamentos que continham discos de *E. globulus e H. dusenii* apresentaram as menores taxas de fragmentação (4,84 ± 0,36 e 3,12 ± 0,64 mg.dia^{-1}, respectivamente) e estas não diferiram estatisticamente (Figura 1).

As taxas produção de MOPF também diferiram entre os tratamentos (F = 10,30, p < 0,01). Os valores observados nos tratamentos que continham os discos de *M. chartacea* e *H. dusenii* (1,87 ± 0,30 e 2,94 ± 1,67 mg.dia^{-1}, respectivamente) foram maiores que os observados nos tratamentos que continham os discos de *E. globulus* e *M. lineata* (0,58 ± 0,11 e 0,34 ± 0,07 mg.dia^{-1}, respectivamente) (Figura 2).

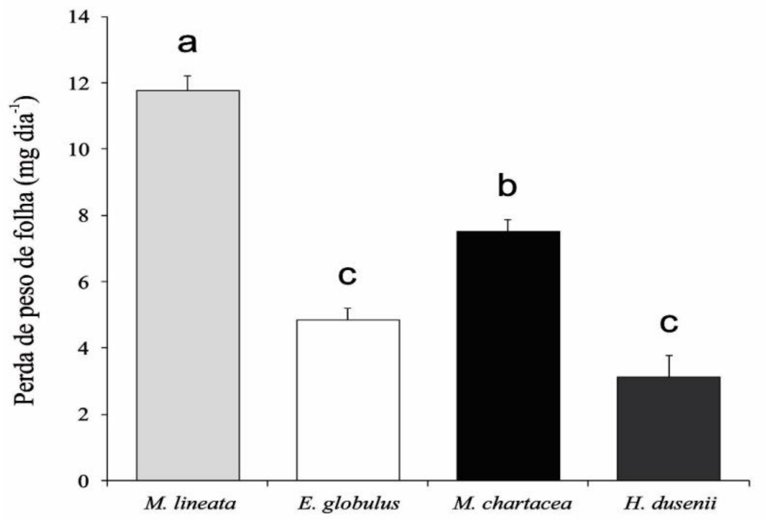

Figura 1. Taxa de fragmentação (mg.dia^{-1}) apresentadas pelos indivíduos de *Trichodactylus fluviatilis* quando expostos separadamente aos detritos *Myrcia lineata*, *Eucalyptus globulus*, *Miconia chartacea* e *Hoffmannia dusenii* condicionados por 10 dias no córrego Macuco. n = 10.

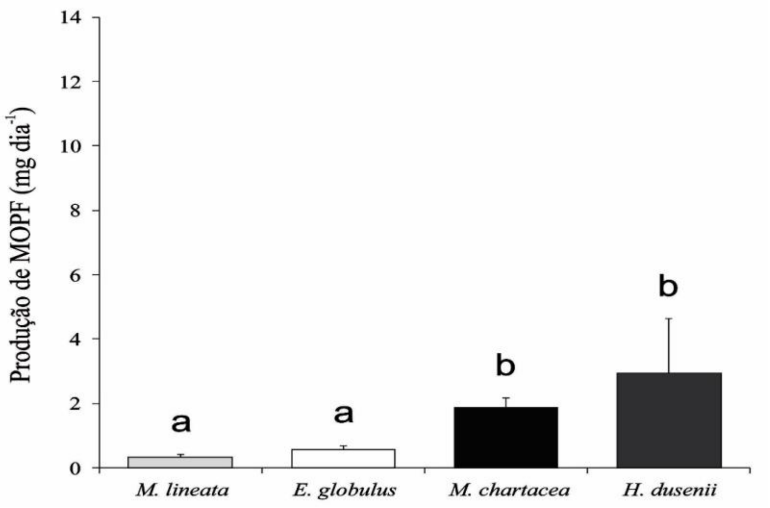

Figura 2. Taxa de produção de MOPF (mg.dia^{-1}) apresentadas pelos indivíduos de *Trichodactylus fluviatilis* quando expostos separadamente aos detritos *Myrcia lineata*, *Eucalyptus globulus*, *Miconia chartacea* e *Hoffmannia dusenii* condicionados por 10 dias no córrego Macuco. n = 10.

Comportamento alimentar de T. fluviatilis

O experimento de comportamento alimentar revelou que os indivíduos de *T. fluviatilis* escolheram os itens alimentares de forma aleatória. A frequência de observação dos caranguejos em um dos itens alimentares não diferiu de 50% em nenhuma das combinações testadas, i.e., detritos vs. larvas, *M. chartacea* vs. *H. dusenii*, e *P. major* vs. *T. gracilis* (Tabela 2). Além disso, as frequências de observação dos caranguejos que escolheram as larvas e não trocaram por detritos foliares e que escolheram *P. major*, espécie que possui o abrigo mais vulnerável a predação, e não trocaram por *T. gracilis* também não diferiu de 50% (Tabela 2).

Tabela 2. Comparações na frequência de escolha dos indivíduos de *Trichodactylus fluviatilis* por um dos itens alimentares oferecidos nos tratamentos do experimento de comportamento alimentar realizados pelo teste *z* de proporções. Pi = proporção observada no primeiro item alimentar. IC = intervalos de confiança (95%).

Tratamentos	**p_i**	**IC**	**Z**	**P**
Larvas vs. Detritos	0,48	0,33; 0,64	- 0,16	0,873
M. chartacea vs. *H. dusenii*	0,60	0,29; 0,90	0,63	0,527
P. major vs. *T. gracilis*	0,60	0,29; 0,90	0,63	0,527
Preferiram larvas e não trocaram por detritos	0,33	0,11; 0,55	-1,41	0,157
Preferiram *P. major* e não trocaram por *T. gracilis*	0,41	0,13; 0,69	-0,58	0,564

Ao final do experimento, a taxa de sobrevivência das larvas de *T. gracilis* foi maior que a das larvas de *P. major*, indicando maior predação de *P. major* pelos caranguejos (Figura 3). Nos tratamentos em que *T. fluviatilis* estava presente juntamente com as larvas e os detritos foliares, as taxas de sobrevivência de *T. gracilis* foi de 88,3% enquanto a de *P. major* foi de 68,0%. Este padrão também se repetiu no tratamento em que as larvas das duas epécies foram oferecidas (*T. gracilis*: 90%; *P. major*: 43,3%).

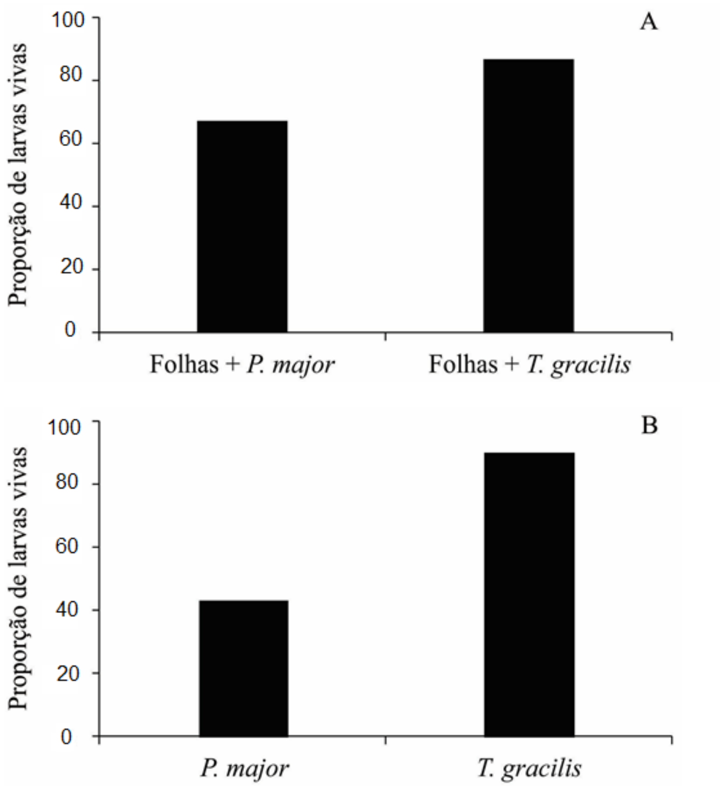

Figura 3. Taxa de sobrevivência (%) das larvas de *Phylloicus major* e *Triplectides gracilis* quando oferecidas aos indivíduos de *T. fluviatilis* com detritos foliares (A, n = 20) e quando oferecidas em conjunto (B, n = 10).

DISCUSSÃO

Os detritos foliares foram processados de forma diferente pelos indivíduos de *T. fluviatilis*. As maiores taxas de fragmentação foram observadas nos tratamentos que continham *M. lineata* e *M. chartacea*, apesar destes detritos apresentarem elevados teores de componentes estruturais e baixos valores nutricionais. As taxas de produção de MOPF também diferiram entre os tratamentos, sendo que *M. chartacea* e *H. duseni* apresentaram os maiores valores. O experimento de comportamento alimentar revelou que os indivíduos de *T. fluviatilis* escolheram os itens alimentares de forma aleatória, entretanto, a taxa de sobrevivência de *T. gracilis* foi maior que a de *P. major*. Estes resultados sugerem que a qualidade dos diferentes itens alimentares não influenciou a preferência alimentar de *T. fluviatilis*.

Vários estudos demonstraram a importância da qualidade química dos detritos na determinação dos padrões de colonização e preferência alimentar de invertebrados fragmentadores em ambientes aquáticos (Lewis, 2007; Li & Dudgeon, 2008; Colpo *et al*., 2012; Jabiol & Chauvet, 2012). Contudo, no experimento de fragmentação, os indivíduos de *T. fluviatilis* processaram maiores quantidades dos detritos mais duros (*M. lineata* e *M. chartacea*). Esses resultados corroboram os resultados obtidos por Costa *et al.* (2016) que, ao avaliarem o comportamento alimentar desta espécie na presença de larvas de insetos fragmentadores, observaram maiores taxas de perda de peso do detrito foliar de menor qualidade nutricional. Possivelmente, este comportamento está associado à estrutura bucal desses organismos; a presença de apêndices preênsis, como maxilas e mandíbulas (Ceccaldi, 1989), facilitaria o consumo de detritos mais duros (*M. chartacea* e *M. lineata*). Estas observações diferem do padrão que tem sido observado para larvas de insetos fragmentadores em riachos tropicais, que exibem preferência por consumir detritos mais macios (Graça *et al.,* 2001; Motomori *et al.,* 2001; Casotti *et al*., 2014; Kiffer *et al*., 2016).

As taxas de produção de MOPF observadas nos tratamentos de cada detrito foliar não foram correlacionadas com as taxas de fragmentação. Por exemplo, as maiores taxas de produção de MOPF não foram observadas nos tratamentos que continham detritos que foram mais fragmentados (*M. lineata*), mas sim no tratamento que continha detritos de *H. dusenii*. Estes resultados sugerem que os caranguejos consomem e/ou assimilam maior quantidade dos detritos de *M. lineata*), incorporandoos em sua biomassa (Cummins *et al*., 1973; Abelho, 2001; Carvalho & Uieda, 2010). Em contrapartida, a maior produção de MOPF nos tratamentos que continham detritos de *H. dusenii*, pode ter resultado do menor consumo deste recurso alimentar pelos indivíduos de *T. fluviatilis*. Apesar dos detritos de *H. dusenii* terem apresentado maior qualidade nutricional, a manipulação destes detritos pelos caranguejos pode ter sido limitada pelos baixos valores de dureza dos mesmos (Costa *et al*., 2016).

No experimento de comportamento alimentar, os indivíduos de *T. fluviatilis* não exibiram preferência por um dos itens alimentares oferecidos e nenhuma das combinações testadas, de forma que a frequência de observações dos caranguejos em um dos itens alimentares não diferiu de 50%. Dado que os itens alimentares não estavam visualmente perceptíveis, estes resultados sugerem que os caranguejos não foram atraídos por estímulos sensoriais (visuais ou químicos), como é comumente reportado na literatura para crustáceos dulcícolas (Burks & Lodge, 2002; Covich, 2015). Uma vez que os caranguejos dulcícolas são organismos que apresentam hábitos oportunistas (Williner & Collins, 2013), nós esperávamos que os mesmos fossem observados com maior frequência no item alimentar de maior qualidade em cada tratamento. Além disso, caso os mesmos fossem inicialmente observados no item de menor qualidade, nos esperávamos que eles fossem trocar de item alimentar nas observações posteriores. No entanto, estas predições não foram corroboradas.

Os caranguejos da família Trichodactylidae são onívoros, podendo consumir grande quantidade de matéria vegetal. No entanto, os recursos de origem animal representam uma fração importante de seu espectro trófico (Collins *et al*., 2006; Pirela & Rincón, 2013; Williner & Collins, 2013). Durante o experimento de comportamento alimentar, foi observada a predação de larvas das duas espécies por *T. fluviatilis*, apesar de ambas apresentarem boas estratégias de camuflagem nos acúmulos de detritos foliares, bem como diferentes períodos de forrageamento em relação aos crustáceos (Williams *et al.,* 1987; Boyero *et al*., 2006; Camargos & Pes, 2011). Além disso, a menor sobrevivência das larvas de *P. major* corrobora a hipótese de que o seu abrigo, por ser construído com detritos foliares (Wantzen & Wagner, 2006, Moretti *et al*., 2009), proporcionaria menor proteção que o abrigo utilizado pelas larvas de *T. gracilis*. Estas últimas caracterizam-se por utilizar pedaços de gravetos de diferentes tamanhos como abrigo (Williams *et al*., 1987). Além de auxiliar nas trocas gasosas direcionando o fluxo d’água para as brânquias, o abrigo confere-lhes uma proteção extra contra predadores, incluindo macroconsumidores (Costa *et al*., 2016).

As informações aqui apresentadas complementam estudos prévios relacionados à participação de *T. fluviatilis* no fluxo de energia de ecossistemas lóticos tropicais. Apesar da qualidade dos itens alimentares não ter influenciado o comportamento alimentar de *T. fluviatilis*, os resultados obtidos indicaram que os crustáceos fragmentam os detritos com qualidades inferiores, recursos que são muitas vezes rejeitados pelos fragmentadores típicos de ambientes lóticos. Além disso, em face da escassez de experimentos envolvendo Trichodactylideos, contribuímos para um melhor entendimento sobre o papel dos crustáceos no processamento de detritos vegetais em ambientes aquáticos tropicais, bem como, contribuir em futuros estudos relacionados à interação trófica desses macroconsumidores com o restante da cadeia trófica.

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CONCLUSÕES DA TESE

Os resultados apresentados nessa Tese suportam o uso de ambas as variáveis corporais avaliadas (comprimento e largura da carapaça), principalmente no modelo *power*, como preditores da biomassa de *T. fluviatilis*. Nossos resultados não indicam diferenças nas nos modelos determinados para machos e fêmeas nas duas populações estudadas, sendo que uma única relação comprimento-biomassa pode ser usada para indivíduos de ambos os sexos. No entanto, as diferenças encontradas nas equações determinadas para as populações amostradas nos riachos do Macuco e Mestre Álvaro sustentam a especificidade dessas relações e a necessidade de determinar uma equação para cada população estudada.

As análises de conteúdo estomacal de *T. fluviatilis* suportam o potencial de participação de *T. fluviatilis* no processo de fragmentação das folhas e demonstraram que, apesar das altas abundâncias de algas e FPOM no conteúdo, os adultos desta espécie têm potencial para alimentar tanto da matéria orgânica disponível nos corpos d'água quanto as larvas invertebrados fragmentadores. As taxas de decomposição das folhas e a produção de FPOM não diferiram entre tratamentos dos fragmentadores ou entre as espécies vegetais. Assim, a hipótese proposta, de que as taxas de decomposição seriam menores quando ambos organismos estivessem juntos, foi parcialmente corroborada uma vez que as taxas de decomposição não alteraram entre os tratamentos.

Contrariamente a maioria das larvas de insetos fragmentadoras presentes em riachos tropicais, os indivíduos de *T. fluviatilis* processam de forma mais significativa os detritos foliares com maior dureza. Estes resultados sugerem que os componentes estruturais e nutricionais dos detritos presentes nesses ecossistemas não influenciam no comportamento alimentar desses organismos, uma vez que são providos de estruturas bucais adapatadas para fragmentação desses recursos de menor qualidade. A hipótese proposta, de que a qualidade dos detritos influenciaria a capacidade de fragmentação de *T. fluviatilis* e que estes iriam preferir se alimentar das larvas ao invés de detritos não foi corroborada. Os resultados demonstraram que a capacidade de fragmentação dos crustáceos não foi diretamente proporcional à qualidade dos detritos foliares, bem como a escolha entre os dois recursos, que se deu de forma aleatória.

A larvas de *P. major* foram mais predadas que as de *T. gracilis*. Esse resultado pode ser justificado devido à maior proteção que os abrigos utilizados pelas larvas de *T. gracilis* (pedaços de gravetos) lhe conferem. Apesar da eficiente camuflagem que os detritos constituintes dos abrigos de *P. major* apresentam, sua predação deu-se de forma mais representativa, corroborando a hipótese proposta ao experimento, a qual os indivíduos iriam preferir as larvas com abrigos de folhas.

Nesse contexto, com a realização desta tese foram apresentadas novas informações sobre o comportamento alimentar e a capacidade de fragmentação de *T. fluviatilis*. Os resultados aqui apresentados representam o ponto de partida para o maior entendimento da influência desta espécie no processo de decomposição de matéria orgânica em riachos tropicais e incrementam dados referentes à ecologia e biologia de crustáceos dulcícolas. Desta forma os resultados desta tese poderão subsidiar a elaboração de novos experimentos nesta linha de pesquisa e, ao mesmo tempo, fornecer bases para a conservação e o manejo das zonas ripárias em trechos de nascentes.

PERSPECTIVAS FUTURAS

Na literatura atual, há uma escassez de estudos sobre a biologia bem como a ecologia da maioria das espécies de caranguejos de água doce, especialmente no caso de *T. fluviatilis*. Neste contexto, pouco se conhece sobre a influência de organismos detritívoros (p.ex. crustáceos) sobre a comunidade aquática a qual se insere, principalmente em regiões tropicais. Sendo assim, estudos que avaliem sua influência são de extrema importância, pois além de permitirem o maior conhecimento de uma determinada população, podem também auxiliar na manutenção desta, caso seja vulnerável ou suscetível à extinção.

Estudos abordando o fluxo de energia em ecossistemas, usualmente quantificam e/ou qualificam a transferência de matéria e energia através de análises de conteúdo estomacal (ACE) ou mesmo pela observação direta da seleção do alimento pelo predador no ambiente. No entanto, deve-se considerar que os itens ingeridos apresentam composições químicas distintas, o que implica velocidades diferentes de digestão e, conseqüentemente, incertezas na identificação do item realmente consumido. Outro fator deve-se à real assimilação do alimento consumido, pois nem todos os itens ingeridos pelo animal serão efetivamente assimilados. Sendo assim, experimentos que realizem análises da ocorrência natural de isótopos estáveis (AIE), especialmente aquelas de carbono e nitrogênio, têm se intensificado em ecologia. Esta técnica vem auxiliando a delinear e a melhor compreender a dinâmica trófica entre os organismos produtores, consumidores e decompositores nas teias alimentares. Assim, a conjunção de ambas as técnicas, ACE e AIE, pode fornecer uma visão ampla e eficaz do fluxo de energia em teias alimentares complexas, como verificado em ambientes tropicais.

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